THE EFFECTS OF PREDATOR EXCLOSURES ON WILSON'S PLOVER *(CHARADRIUS WILSONIA)* NEST SUCCESS AND PRODUCTIVITY

by

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(Under the Direction of Robert J. Cooper)

ABSTRACT

Predator exclosures have been utilized as a technique to increase breeding productivity among several ground-nesting bird species. The effect of predator exclosures on Wilson's Plover (*Charadrius wilsonia*) nest success and productivity was studied on Little St. Simons Island, Georgia during the 2016 and 2017 breeding seasons. Exclosures successfully excluded mammalian and avian predators. Nests with exclosures had a significantly higher daily survival rate than unexclosed nests in both breeding seasons. Significantly more chicks hatched and fledged per nesting attempt from the exclosed treatment group than the control group in 2017, but estimates for both treatments were similar 2016. The survival probabilities for chicks were not significantly different between treatments. If every Wilson's Plover nest was protected with an exclosure the population growth rate was estimated to be in decline. Although exclosures can help increase productivity, additional predator management is necessary to maintain viable populations of beach-nesting shorebirds in this region.

INDEX WORDS: Wilson's Plover, Shorebird management, Predator management, Predator exclusion, Little St. Simons Island, Nest success, Chick survival

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CHAPTER 1

INTRODUCTION

BACKGROUND

Numerous species of beach-nesting shorebirds are currently experiencing threats and challenges to their survival and viability. Some of these threats are increased predation pressures, habitat loss and degradation, human disturbance, and hunting, and may occur across their entire annual life cycle. Many of these birds have had large parts of their breeding grounds destroyed or modified by anthropogenic activities, such as coastal development and shoreline modification (Winn et al. 2013). These disturbances can result in low breeding productivity, reduced breeding ranges, and population declines.

The Wilson's Plover (*Charadrius wilsonia*) is a migratory coastal breeding shorebird that is facing some of these threats, especially on its breeding grounds. This species nests solely in coastal beach habitats, and unlike other threatened plover species, do not have any inland breeding populations (Corbat and Bergstrom 2000). Their range has contracted over the last century, and now they are no longer found breeding north of Virginia (Zdravkovic 2013). As a result, the species is listed on the U.S. Shorebird Conservation Plan as a "Species of High Concern (Category 4)" (Brown et al. 2001). Though Wilson's Plovers have no federal protection above that of any migratory bird species, several states have designated the species for protection (Corbat and Bergstrom 2000). In Georgia, Wilson's Plovers are listed as "Threatened", and only 300 nesting pairs were estimated in the state in 2010 (Sterling 2017). One of the largest threats to

Wilson’s Plovers in Georgia is predation by wild, feral, and domesticated animals (GADNR 2010).

Predator management is a controversial but valuable technique often used to increase shorebird and seabird breeding productivity and survival. A reduction in predator populations can have positive effects on nest survival of wading birds (Bolton et al. 2007, Fletcher et al. 2010, Nordström et al. 2003, Smith et al. 2010, Tharme et al. 2001), however, lethal predator management can be costly, controversial, and time consuming (Armstrong et al. 2006, Bolton et al. 2007, Duebbert and Lokemoen 1980, Smith et al. 2010, Tapper et al. 1982). Predator exclusion techniques, such as predator exclosures at nest sites, are a non-lethal alternative management approach for protecting ground-nesting birds (Smith et al. 2011). A predator exclosure is a large wire cage that is placed over individual nests, which permits incubating adults to travel freely in and out (Murphy et al. 2003). Meso-predators are unable to access eggs in the center of the exclosure, and a top netting prohibits birds of prey from entering as well. Though predator exclusion is one of the most widely used methods for increasing nest success for ground-nesting birds (Gibbons et al. 2007), predator exclosures have only minimally been used and studied with Wilson’s Plovers (e.g., DeRose-Wilson et al. 2013).

We conducted research examining the effects of predator exclosures on Wilson’s Plover nest success. This is the first intensive study that focused solely on the efficacy of predator exclosures with this species. This project was a demonstration site for a broad-scale Best Management Practice (BMP) study examining predator management efforts on shorebird conservation and management. The goal of the BMP study was to provide managers with information on how to successfully implement predator management at their sites for the benefit of shorebirds.

STATEMENT OF RESEARCH QUESTION

Wilson’s Plovers are a vulnerable, coastal-breeding species, and management activities need to be tested to see if they increase Wilson’s Plover productivity and population size. The goal of this project is to determine the effects of predator exclosures on Wilson's Plover productivity, and assess how this management approach may influence their Atlantic Coast population.

SIGNIFICANCE OF STUDY

Wilson's Plovers have been suggested as an indicator species for overall coastal ecosystem health (Zdravkovic 2013). An indicator species is “an organism whose presence, absence or abundance reflects a specific environmental condition,” thus helping assess the health of the ecosystem the species occurs in (McDonough et al. 2012). Shorebirds are sensitive to anthropogenic activities, and decreased survival in shorebirds has been attributed to human disturbance (Winn et al. 2013). Human disturbance also can result in artificially overabundant predator populations at shorebird breeding sites (Rees et al. 2015).

The overarching goal for the Atlantic Flyway Shorebird Conservation Business Strategy is to increase 15 focal shorebird populations, including Wilson's Plovers, by 10% by 2025. Focal species were selected because they are “highly imperiled or of high concern, represent important habitat suites in the flyway, and have existing conservation plans to make implementation more practical.” The Wilson’s Plover is a focal species due to a high priority status, and it is a temperate beach nesting representative. One approach to accomplishing the Atlantic Flyway Shorebird Conservation Business Strategy’s goal for Wilson’s Plovers is to minimize predation on breeding grounds from native, non-native, and domestic wildlife in the next 3-5 years. The strategy suggests implementing new predator control methods to maximize effectiveness of reducing threats to shorebird populations (Andres et al. 2015).

Predator exclosures are a novel management approach for Wilson’s Plovers on the Georgia coast. Although currently used for other plover species, the effectiveness of predator exclosures needs to be assessed before this management technique is broadly deployed with this species. The results and management recommendations from this research project will benefit shorebird conservationists and managers across the breeding range of Wilson's Plovers. If predator exclosures are proven to be an effective technique, then they can be deployed at breeding sites as an alternative to lethal removal to increase nesting productivity. An increase in nesting productivity can assist with stabilizing or increasing Wilson’s Plover populations.

THESIS STRUCTURE

In Chapter 2 of this thesis, a comprehensive literature review regarding components of this research study is presented. The literature review encompasses Wilson’s Plover life history and prior research studies, prior studies related to predator exclusion with ground-nesting birds, studies modeling shorebird populations affected by different management scenarios, and ghost crab life history.

Chapter 3 is formatted as a manuscript, and will be a multi-authored document submitted for publication in a scientific journal. We estimated the daily survivorship rate between Wilson’s Plover nests treated with predator exclosures and unexclosed nests, chick survivorship and fledgling rates, and how the predator exclosure management technique could affect their Atlantic Coast population. A description about predator activity through trail camera observations is included in this section as well.

Finally, in Chapter 4, I summarize the conclusions of this research study, and discuss the priorities for future research. Also, I present management recommendations for the use of predator exclosures with Wilson’s Plovers.

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CHAPTER 2

LITERATURE REVIEW

WILSON'S PLOVER LIFE HISTORY

The Wilson's Plover (*Charadrius wilsonia*) is a migratory shorebird that is found solely in coastal habitats. The species is distinguished from other plover species by its heavy, black bill, white underparts, grayish brown upperparts, and dark neck ring (Corbat and Bergstrom 2000). There are three recognized subspecies that vary, *C. w. wilsonia*, *C. w. cinnamonius*, and *C. w. beldingi* (Ridgway 1919, Hellmayr and Conover 1948, Blake 1977). Each subspecies varies in coloration and geographic location. *C. w. cinnamonius* ranges year-round from the southern Carribean to northern South America, and the Lesser Antilles. *C. w. beldingi* breeds along the Pacific Coast from Baja California to Panama. Its wintering range overlaps with the breeding range while also extending further south into Peru. *C. w. wilsonia* can be found breeding on the Atlantic Coast from Virginia to Florida, U.S. and Mexico Gulf Coast, Belize, Bahamas, and Greater Antilles, and wintering on the Gulf Coast to north and east South America (Ridgway 1919). Historically, Wilson's Plovers occurred north of Virginia, but in the past 100 years their breeding range has contracted (Zdravkovic 2013). The last Wilson's Plover nest record in Maryland was in 1985 (Hoffman 1996). *C. w. wilsonia* (hereafter, "Wilson's Plover") is the focal subspecies of this study.

Breeding Wilson's Plovers have established territories and begin nesting by mid-April in Georgia (Corbat 1990). This medium sized plover nests in scrapes on the ground (Bergstrom 1982), and in a variety of beach habitats including "salt flats, coastal lagoons, sand dunes, newly accreted beach, dry sand beach above tidal area, overwash areas, and predunes" (Tomkins 1944, Corbat 1990, Corbat and Bergstrom 2000). Males initiate scrape construction, and will create several scrapes for the female to decide which she prefers to lay eggs in (Bergstrom 1988b). Eggs are cryptic and highly camouflaged with the sandy substrate as they are often cream-colored with dark blotches (Baicich and Harrison 1997). Clutch size is typically three eggs (Bergstrom 1988a, Corbat 1990), and pairs will renest after a previous nest failure (Corbat and Bergstrom 2000). Average incubation is 25 days after the last egg is laid (Bergstrom 1988a, Corbat 1990).

Wilson's Plover chicks are precocial (Corbat and Bergstrom 2000) and are able to walk as soon as 1-2 hours after hatching (Bergstrom 1988a). Chicks remain with protective parents after hatching (Bergstrom 1988a) and are able to feed themselves. Young are downy, and are highly camouflaged with sandy and rocky habitats as well. No information is known regarding Wilson's Plover chick growth (Corbat and Bergstrom 2000). In Georgia, period survivorship for chicks was estimated at 0.78 (Sterling 2017).

Time to fledgling has not been well studied in Wilson's Plovers. Tomkins (1944) observed a 21-day old unfledged chick, and reported a minimum of 21 days required for fledging. A single brood's fledging chronology was documented for the first time in 2006 (Zdravkovic 2010). Zdravkovic (2010) reports a 33-day old chick was able to fly short, 20-m distances, and at 35 days of age, the same chick was capable of 75-m flights. Zdravkovic (2010) estimates the amount of time required for fledgling is approximately 31-35 days, and varies by brood and habitat type. Some chicks could sustain short flights as early as 30 days. If disturbance is low and food abundance is high then young may not have the pressure to initiate flight. In these situations, young may not fledge until after 35 days of age (Zdravkovic 2010). Another study reports fledgling age in North Carolina is 28 days (Ray 2010). In Georgia, chicks observed after 35 days were documented as fledged (Sterling 2017).

CURRENT STATE OF KNOWLEDGE

Several basic research studies in the 1980's and early 1990's from Bergstrom (1981, 1982, 1986, 1988a, 1988b, 1989) and Corbat (1990) provided a foundation of information on the natural history and breeding biology for the species. Other studies conducted in the Caribbean and Venezuela contributed research on Wilson's Plover activity budgets, nest site selection, and habitat use (Morrier and McNeil 1991, Thibault and McNeil 1994, Brown and Brindcock 2011).

In recent years, Derose-Wilson et al. (2013, 2015) studied Wilson's Plover nest-site selection, demography, and effects of civilian and military overflights on heart rate and behavior on a North Carolina barrier island. The authors estimated fledging probability to be 74%, which resulted in a 0.78 fledglings/pair reproductive output. In addition, this study was one of the first publications to estimate juvenile and adult survivorship. The estimated apparent annual adult survival was 77%, and the apparent annual juvenile survival was 42% based on resighting rather than mark-recapture modeling (DeRose-Wilson et al. 2013). Regarding overflights, Wilson's Plovers scanned more during periods of civilian and military fixed-wing overflights than during periods without this disturbance. Though plovers were alert, their heart rates and incubation rates did not change during periods of overflight (DeRose-Wilson et al. 2015). The effects and consequences of human disturbance on shorebird behavior and productivity is of increasing concern to biologists.

Sanders et al. (2012) addressed the abundance and distribution of breeding Wilson's Plovers in South Carolina, a "threatened" species for the state (Corbat and Bergstrom 2000). Of the approximately 376 breeding pairs in South Carolina, 29% were recorded on private land and

71% were recorded on public land. The authors stressed the importance of focusing conservation efforts on Wilson's Plovers since 79% of South Carolina's breeding pairs nested in beach habitats. Often beach-nesting birds share their breeding habitat with beach visitors and are disturbed by recreational activities.

In Georgia, Sterling (2017) examined the relationship of spatial and habitat characteristics on Wilson’s Plover productivity and site selection. She assessed how nest-site selection and success varied with habitat features, evaluated how predation and overwash influenced nest success, and estimate chick survivorship. Little St. Simons Island was a study site used in this research study. The data collected from this project provided a baseline of knowledge regarding Wilson’s Plovers at this breeding location for my thesis research.

There have been several recent attempts at a Wilson’s Plover census. The entire *C. w. wilsonia* population is estimated to be roughly 6,000 individuals (Brown et al. 2001). Other reports indicate there are approximately 8,600 breeding individuals in the United States alone with 2,000-2,200 individuals in the Atlantic Coast population and 6,000-6,4000 individuals in the Gulf Coast population (Zdravkovic 2013). For *C. w. cinnamonius* and *C. w. beldingi*, population data does not currently exist (Zdravkovic 2013).

There is still a lot of missing information that is needed to understand and effectively conserve Wilson’s Plovers. Rigorous estimates of adult survivorship and lifespan, causes of adult mortality and regional population trends are still unknown (Corbat and Bergstrom 2000). Surveys that attempted a complete census did not cover the entire breeding and wintering range, so populations were estimated where there were spatial gaps, such as Mexico or the Carribean, (Zdravkovic 2013). There is low confidence in the current Wilson’s Plover population estimate

(Brown et al. 2001). Much more research across the Wilson's Plovers entire range is needed, and almost any research would be beneficial to their conservation and management.

PREDATOR EXCLUSION STUDIES

Predation is the leading cause of nest mortality among birds (Ricklefs 1969). Several predator species, such as raccoons (*Procyon lotor*) and Fish Crows (*Corvus ossifragus*), are attracted to beaches by human presence. Over time, these predators become overpopulated and depredate shorebird eggs and chicks at a rate that decreases bird populations (Rees et al. 2015). High predation is one of several significant threats to shorebird populations listed in shorebird conservation plans (Brown et al. 2001, Winn et al. 2013).

Reducing avian and mammalian predator populations can have positive effects on wader nest survival (Tharme et al. 2001, Nordström et al. 2003, Bolton et al. 2007, Fletcher et al. 2010, Smith et al. 2010). However, lethal predator management is a controversial management approach due to animal welfare issues (Smith et al. 2010). Additionally, lethal control is time-consuming, expensive, may only have short-term effects, and does not always result in an increase in the prey population (Duebbert and Lokemoen 1980, Tapper et al. 1982, Armstrong et al. 2006, Bolton et al. 2007, Smith et al. 2010).

One alternative to lethal predator control for the protection of breeding birds are predator exclosures, which have been used as a management tool for the conservation of several species of ground-nesting birds (Smith et al. 2011). A predator exclosure is a large wire cage that is placed over individual nests, which permits incubating adults to travel freely in and out (Murphy et al. 2003b). Meso-predators, such as raccoons (*Procyon lotor*), are unable to access eggs in the center of the exclosure, and a mesh top prohibits birds of prey from entering as well (Melvin et al. 1992). Since predator exclosures are deployed around active nests, adults are disturbed during the set-up process and incubation. However, Tan et al. (2015) examined stress levels of incubating birds, and discovered there was no increase in stress levels of birds incubating nests with predator exclosures.

The effects of predator exclosures have been studied with several shorebird species, including Piping Plovers (*Charadrius melodus*) (Rimmer and Deblinger 1990, Deblinger et al. 1992, Melvin et al. 1992, Vaske et al. 1994, Mabee and Estelle 2000, Larson et al. 2002, Murphy et al. 2003a, 2003b, Maslo and Lockwood 2009, Barber et al. 2010, Doherty and Heath 2011, Beaulieu et al. 2014, Stringham and Robinson 2015), Snowy Plovers (*Charadrius nivosus*) (Mabee and Estelle 2000, Neuman et al. 2004, Hardy and Colwell 2008, Dinsmore et al. 2014, Pearson et al. 2016), Killdeer (*Charadrius vociferous*) (Nol and Brooks 1982, Mabee and Estelle 2000, Johnson and Oring 2002), Northern Lapwings (*Vanellus vanellus*) (Isaksson et al. 2007, Malpas et al. 2013), Common Redshanks (*Tringa tetanus*) (Isaksson et al. 2007), St. Helena Plovers (*Charadrius sanctaehelenae*) (Burns et al. 2013), Pectoral Sandpipers (*Calidris melanotos*) (Estelle et al. 1996), Southern Dunlin (*Calidris alpine schinzii*) (Pauliny et al. 2008), and Western Sandpipers (*Calidris mauri*) (Niehaus et al. 2004). The only peer-reviewed published study that deployed predator exclosures at Wilson's Plovers' nests was in North Carolina (DeRose-Wilson et al. 2013). DeRose-Wilson et al. (2013) deployed predator exclosures around 17 Wilson's Plover nests during the study, and found exclosed nests had a higher daily survival rate than nests without exclosures. However, testing the effectiveness of predator exclosures at increasing Wilson's Plover productivity was not the primary focus of this study.

There are conflicting assessments on the overall benefit of predator exclosures on nest success of Piping Plovers, though most publications indicate a beneficial effect (Smith et al.

2011). Maslo and Lockwood (2009) observed a significant increase in nest hatching success among nests with exclosures than nests without exclosures and nests protected by electrified fencing after analyzing 10 years of data compiled by New Jersey Division of Fish and Wildlife Endangered and Nongame Species Program. Deblinger et al. (1992) evaluated different exclosure designs and sizes, and reported an "overwhelming majority" of exclosure designs are effective at protecting nests from predators. Exclosure characteristics that had a higher probability of nest predation included fencing < 122 cm (predicted probability = 0.42) than fencing ≥ 122 cm (predicted probability = 0.08) in height, and square designs (predicted probability = 0.72) versus circular (predicted probability = 0.08) or triangular designs (predicted probability = 0.00). During one of the earliest exclosure studies on Cape Cod, 26 nests were treated with exclosures and had a higher hatching rate than 24 untreated nests (Rimmer and Deblinger 1990). Another study on Cape Cod reported the daily survival rate was significantly higher for exclosed nests (0.994) than unexclosed nests (0.930) (Melvin et al. 1992). Doherty and Heath (2011) also had a higher hatching success among nests with exclosures on Eastern Long Island beaches. In North Dakota and Montana, Murphy et al. (2003a) tested three management techniques; no nest protection, nest cages, and nest cages with electric fencing. Results showed the predator exclosure cages increased Piping Plover reproductive success, and there was no significant difference in production between just nest cages and both nest cages within electric fencing.

The increase in Piping Plover hatching success from predator exclosures translates to Snowy Plovers as well. Hardy and Colwell (2008) reported a significant increase in nest success among beach nesting Snowy Plovers with exclosures. Exclosed Snowy Plover nests had a higher daily survival rate than unexclosed nests in Pearson et al.'s (2016) study, however, nesting areas with high predation and minimal human disturbance were targeted. Additionally, Neuman et al. (2004) described a higher hatching success among nests with predator exclosures versus unexclosed nests. The study was divided into a pre-management phase without exclosure use, and a management phase in which exclosures were deployed. During the pre-management phase, hatching success decreased from 66% to 26%, but increased to a mean hatching rate of 68% during the management phase. When 19 years of nesting data were analyzed from breeding Snowy Plovers in Oregon, researchers found apparent nesting success was higher among nests with exclosures (68%) than nests without exclosures (25%). Small exclosures, large exclosures, and fencing outfitted with electric wire were evaluated for this study that included 1,951 nests (Dinsmore et al. 2014).

Though these studies reported an increase in hatching success among nests deployed with exclosures, some additionally reported there was no increase in overall productivity. During Hardy and Colwell's (2008) study there was no difference in fledging rates between nests treated with exclosures and nests without exclosures. Fledging rates only varied between study sites. Neuman et al. (2004) reported the higher hatching success among Snowy Plover nests with exclosures did not render an increase in the number of chicks produced or fledging success. Fledging rates did not differ between exclosed and unexclosed treatments in Dinsmore et al.'s (2014) study either.

A few studies reported either no effect or a negative effect of predator exclosures on shorebird nest success. Mabee and Estelle (2000) found no significant difference in daily survival rate between nests protected with predator exclosures and unprotected nests among Piping Plovers (*n* = 5 protected, 4 unprotected), Snowy Plovers (*n* = 13, 14 and *n* = 14, 14), and Killdeer (*n* = 7, 9). There were several reasons for nest failures specific to the study area, including cattle trampling, predation by small mammal and snake, and failure by beetles burying into eggs. Exclosures were not effective at increasing nest daily survival rate among breeding St. Helena Plovers. Daily survival rate was not affected by exclosures since smaller feral cats were able to fit through the openings in the exclosures (Burns et al. 2013). Among Killdeer, Nol and Brooks (1982) used a small, 1-m exclosure size, and reported no effect on nest success between treatment groups. Raccoons were able to reach inside the exclosures and grab eggs out of the nests, and mink and long-tailed weasels fit through the exclosure openings to depredate nests as well. The authors recommended a larger exclosure design at breeding sites with raccoon predation, so animals are unable to reach through the openings (Nol and Brooks 1982). Thus, there is still a debate if predator exclosures are an effective tool for plover conservation, and more research needs to be conducted to determine the answer (Mabee and Estelle 2000).

Several studies also have linked predator exclosures to high nest abandonment and adult mortality. Barber et al. (2010) analyzed 22 years of Piping Plover nesting data from Prince Edward National Park, Canada. It was determined that nests with exclosures had a greater nest abandonment rate than unexclosed nests; however, the protected nests showed greater reproductive success as well. Maslo and Lockwood (2009) analyzed another long-term data set and found the abandonment rate for unexclosed, exclosed, and electrified nests to be 7%, 19%, and 30%, respectively. Vaske et al. (1994) observed 10% of all Piping Plover nests abandoned during the study, and examined exclosure construction variables as possible influences. There was a high abandonment of exclosures without posts for support, and weather conditions in Canada, such as high winds, could have moved the exclosures enough to disturb incubating adults. However, the majority of variables, such as time of day and shape of exclosures, did not influence nest abandonment. Since these variables had no effect, predation likely led to nest abandonments.

Often, nest abandonment is a result of the mortality of an incubating adult. Predators are known to target multiple nests within a short time frame, often referred to as “episodic” predation (Murphy et al. 2003a, Neuman et al. 2004, Hardy and Colwell 2008). Hardy and Colwell (2008) described the disappearance of 8 incubating Snowy Plovers with 1 confirmed death by an unknown predator during a single month. Murphy et al. (2003a) conducted their research on lake beaches in Alberta, Saskatchewan, North Dakota, and Montana and attributed the adult mortality likely to raptor depredation since nearby trees were a perch for raptors. A total of 5% of Piping Plover nests monitored with predator exclosures documented an adult mortality event, and most predation occurred in 2-10 day episodes. In contrast, no unprotected nests experienced any adult mortality in the same study, thus predator exclosures were judged to be detrimental to adult survival. Neuman et al. (2004) reported 25 dead Snowy Plovers over the course of the study with 76% of deaths occurring at exclosures. Many of these mortalities were attributed to raptor predation since a Merlin killed 8 Snowy Plover adults over a 12 day period. Beaulieu et al. (2014) found predators to spend more time around exclosed nests in comparison to unprotected nests. This finding suggests that some predators learn to key-in on exclosures. Over 19 years, 41 adult mortalities occurred at exclosures in Oregon; however, the number of deaths at unexclosed nests was unknown, so a comparison between treatments cannot be made (Dinsmore et al. 2014). Mink killed one incubating Killdeer at an exclosure during Nol and Brooks’ (1982) study. Any adult mortality can have a negative effect on a population (Dinsmore et al. 2014), and often adult mortality is the most important factor in determining population viability in shorebirds (Sandercock 2003).

POPULATION MODELING

Population models can predict future population trends over time and can be used as a tool to assess whether management techniques aimed at increasing certain population parameters are likely to be successful. Ryan et al. (1993) conducted one of the earliest stochastic population models on the Great Plains Piping Plover population. At this time, estimates for immature Piping Plover survival rates did not exist, though they did for other closely related species. First year survival rates of Snowy Plovers (Page et al. 1983) and Ringed Plovers (*Charadrius hiaticula*) (Pienkowski 1984) ranged from 71% to 87% of the adult survival estimates, so Ryan et al. (1993) used values corresponding to 70%, 80%, 90%, and 100% of the adult survival estimate. The adult survival rate was estimated at 0.66 (Root et al. 1992), and chicks fledged per pair was 0.86. Only the females were modeled in the population. The model results showed an annual population decline of 13.7%, 10.0%, 7.6%, and 4.7%, and extirpation at 44, 56, 81, and 120 years with each respected immature survival rate. It was determined reproductive output needed to be increased to 1.16-1.19 chicks/pair to achieve a 1-2% population growth. The authors suggested protection of nests and chicks as a strategy to increase reproductive success and growth rates (Ryan et al. 1993).

Population viability models have been created to incorporate parameters affected by the predator exclosure management method. Larson et al. (2002) estimated fledgling success with and without predator exclusion, and revised a stochastic simulation model of the Great Plains Piping Plover demography. The authors attempted to estimate true temporal variation in fledging rates for stochastic population modeling by using the total variance from their longest dataset as an estimate of temporal variability. Mean fledgling rate was estimated under five management techniques, including a no protection (0.73 fledglings/pair), and predator exclusion nest cages

(1.28 fledglings/pair). Annual adult survivorship estimates (0.737) were from the Great Plains population (Larson et al. 2000), but the annual immature survival estimate (0.48) was from the Atlantic Coast population (Melvin and Gibbs 1996). Larson et al. (2002) argued the immature survival rate reported by Larson et al. (2000) for the Great Plains population was underestimated and resulted in rapid declines in simulated populations. In the baseline and current management models, Piping Plover populations declined by 6.2%/year, and 4.3%/year, respectively. To stabilize the finite growth rate (λ), there needed to be 1.44 fledglings/pair produced in alkaline wetlands, which resulted in a population wide median of 1.25 fledglings/pair produced. In the Great Plains population, Piping Plovers nest on alkaline wetlands and rivers, but predator exclusion techniques are primarily deployed at alkaline wetland sites. The authors suggested that if survival rates increase by 4-11% then lambda would only be in a 2% decline. Survival rates may already be underestimated since permanent emigration is treated as mortality in mark-recapture models (Lebreton et al. 1992). Overall, this study indicates that Piping Plover populations can be stabilized or increased if reproductive success is increased by predator management techniques (Larson et al. 2002).

The effect of predator exclosures was also studied on a western Snowy Plover population through a stochastic population viability model (Watts et al. 2012). An episodic predation event on plovers at predator exclosures (Hardy and Colwell 2008) led the authors to model the reduction of adult survival as it relates to the benefits of predator exclusion nest protection. Watts et al. (2012) modified Ryan et al.'s (1993) Piping Plover population model to include a density-dependent immigration variable, clutch size of three eggs, equal sex ratios, and only track the male portion of the population. Beta distributions were used for the adult and juvenile return rates, and number of male fledglings produced to incorporate stochasticity into the model.

Results showed an increase in chick fledgling rates among nest exclosures, but that population benefit may be offset by adult mortality. The model indicated a population decrease when adult mortality increased by 10-20%, and there would be a net negative effect of exclosures if adult survival is 90% of the unexclosed nest rate.

GHOST CRAB LIFE HISTORY

Ghost crabs (*Ocypode sp.*) are one of the largest invertebrates on ocean beaches, and can be found on nearly every sandy coastline around the globe. The Atlantic ghost crab (*Ocypode quadrata*) ranges from Santa Catarina, Brazil to Block Island, Rhode Island on the Atlantic and Gulf of Mexico coasts. Ghost crabs construct complex burrows in the sand, which serve multiple purposes (Lucrezi and Schlacher 2014). Burrows protect ghost crabs from predators and weather elements, and provide a moist environment so crabs avoid desiccation (Byerly and Crowe 1998). Burrows can be as deep as 200cm, and can have an opening diameter as wide as 75mm. The diameter of the burrow is often associated with ghost crab size (Turra et al. 2005, Lucrezi and Schlacher 2014). Burrow openings frequently face the ocean (Clum 2005, Hill 1982), and are distributed unevenly along the beach with the greatest concentrations correlating with areas of high accretion (Clum 2005).

Ghost crabs are active predators and have been documented to feed upon more than 40 taxa of prey species, including the eggs and young of beach-nesting bird species (Lucrezi and Schlacher 2014). Wolcott and Wolcott (1999) claimed that ghost crab predation on shorebird eggs and chicks is opportunistic and does not directly cause low productively at breeding sites. Rather, the authors suggested ghost crabs indirectly affect the survival of shorebird eggs and young by evoking defensive parental behavior that attracts other predators and leaves eggs and young exposed to threats. However, there are several reports that counter Wolcott and Wolcott's

(1999) findings. In Florida, ghost crabs were the most common predator of Snowy Plover eggs, accounting for 64% of depredation events. Snowy Plover nests were more likely to be successful in areas further away from ghost crab burrows. Ghost crabs were responsible for depredation of Wilson's Plover and Least Tern eggs as well (Pruner 2010). Loegering et al. (1995) describes an instance where a ghost crab fed upon an 8-day old Piping Plover chick at the base of its burrow. Though the authors did not observe the ghost crab directly depredate the chick, they were confident that was the cause of the chick's death. Watts and Bradshaw (1995) also reported a ghost crab preyed on a Piping Plover egg.

The relationship between ghost crab presence around shorebird nest sites and nest success was studied closely using Piping Plovers as a study species (Kwon et al. 2018). Kwon et al. (2018) recorded the number of ghost crabs or burrow openings within the vicinity of plover nests, along with several other covariates, such as nest age, reproductive stage, and presence of a predator exclosure. A logistic exposure model (Rotella et al. 2004, Shaffer 2004) was used to estimate the nest daily survival rate. There was a presence of ghost crabs or burrows at approximately 26% of nests with predator exclosures on 2% of the observation days. Overall, the survival of plover nests was lower when ghost crab sign was present, and crabs preyed on 9.6% of all monitored nests in the study. Of exclosed nests, 53% of the 17 nest failures were depredated by ghost crabs. The authors suggested nest protection from ghost crabs could increase nest success, but also note that more research is needed regarding the biological role of ghost crabs in beach ecosystems (Kwon et al. 2018).

SUMMARY

Despite apparent population declines, small overall population size, and status as a species of concern in several states, there are many aspects of Wilson's Plover ecology and conservation that are unknown or minimally studied. These include estimates of adult and juvenile annual survival, life span, and accurate population assessments. While nest exclosures would seem to hold potential as an effective management technique to increase Wilson's Plover nest success, there is uncertainty concerning the potential negative effects of nest exclosures. Hence the need for this study.

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CHAPTER 3

EFFECT OF PREDATOR EXCLOSURES ON WILSON'S PLOVER NEST SUCCESS AND PRODUCTIVITY[1]

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[1] Sample, Gingerella, L.C., A.V. Sterling, T.S. Keyes, S.D. Coleman, and R.J. Cooper. To be submitted to *Journal of Wildlife Management*.

ABSTRACT

Predator exclosures have been utilized as a technique to increase breeding productivity among several ground-nesting bird species. The effect of predator exclosures on Wilson’s Plover (*Charadrius wilsonia*) nest success and productivity was studied on Little St. Simons Island, Georgia during the 2016 and 2017 breeding seasons. Exclosures successfully excluded mammalian and avian predators. Nests with exclosures had a significantly higher daily survival rate than unexclosed nests in both breeding seasons. Significantly more chicks hatched and fledged per nesting attempt from the exclosed treatment group than the control group in 2017, but estimates for both treatments were similar 2016. The survival probabilities for chicks were not significantly different between treatments. If every Wilson’s Plover nest was protected with an exclosure the population growth rate was estimated to be in decline. Although exclosures can help increase productivity, additional predator management is necessary to maintain viable populations of beach-nesting shorebirds in this region.

INTRODUCTION

Numerous species of beach-nesting shorebirds are currently experiencing threats and challenges to their survival and long-term viability. Threats include increased predation pressures, habitat loss and degradation, human disturbance, and hunting, and may occur across their entire annual life cycle. Many breeding grounds have been destroyed or modified by anthropogenic activities, such as coastal development and shoreline modification (Winn et al. 2013). These disturbances can result in low breeding productivity, reduced breeding ranges, and population declines.

Predation is the leading cause of nest failure among birds (Ricklefs 1969), and high predation rates can limit shorebird populations (Brown et al. 2001, Winn et al. 2013). Several predator species, such as raccoons (*Procyon lotor*) and Fish Crows (*Corvus ossifragus*), are attracted to beaches by human presence. These predators can become artificially overpopulated over time and depredate shorebird eggs and chicks at a rate that decreases bird abundance (Rees et al. 2015). The management of overpopulated predators is a challenge for resource managers, though attainable, whereas habitat management to reduce nest predation often is not because of the sheer magnitude of the required actions.

Because of the overabundance of subsidized predators, predator management is now a favored technique to increase beach-nesting bird breeding productivity and survival. A reduction in predator populations can have positive effects on nest survival of wading birds (Tharme et al. 2001, Nordström et al. 2003, Bolton et al. 2007, Fletcher et al. 2010, Smith et al. 2010), but lethal predator management can be costly, controversial, and time consuming (Duebbert and Lokemoen 1980, Tapper et al. 1982, Armstrong et al. 2006, Bolton et al. 2007, Smith et al. 2010). Predator exclusion techniques, such as predator exclosures at nest sites, are a non-lethal alternative management approach for protecting ground-nesting birds (Smith et al. 2011). A predator exclosure is a large wire cage that is placed over individual nests, which permits incubating adults to travel freely in and out (Murphy et al. 2003b). Meso-predators are unable to access eggs in the center of the exclosure, and a top netting prohibits birds of prey from entering as well (Melvin et al. 1992).

The effects of predator exclosures have been studied with several shorebird species, including Piping Plovers (*Charadius melodus*) (e.g., Maslo and Lockwood 2009, Barber et al. 2010, Beaulieu et al. 2014,), Snowy Plovers (*Charadrius nivosus*) (e.g., Hardy and Colwell 2008, Dinsmore et al. 2014, Pearson et al. 2016), Killdeer (*Charadrius vociferus*) (e.g., Nol and Brooks 1982, Mabee and Estelle 2000, Johnson and Oring 2002), Northern Lapwings (*Vanellus vanellus*) (Isaksson et al. 2007, Malpas et al. 2012), Common Redshanks (*Tringa totanus*) (Isaksson et al. 2006), St. Helena Plovers (*Charadrius sanctaehelenae*) (Burns et al. 2013), Pectoral Sandpipers (*Calidris melanotos*) (Estelle et al. 1996), Southern Dunlin (*Calidris alpine schinzii*) (Pauliny et al. 2008), and Western Sandpipers (*Calidris mauri*) (Niehaus et al. 2004). Many of these studies report a beneficial effect of predator exclosures on avian nest success, especially for Piping Plovers (Smith et al. 2011). For example, Maslo and Lockwood (2009) reported a significant increase in nest hatching success among nests with exclosures than nests without exclosures and nests protected by electrified fencing.

Several studies also have linked predator exclosures to high nest abandonment and adult mortality. In Prince Edward National Park, Canada, Piping Plover nests with exclosures had a greater nest abandonment rate than unexclosed nests; however, the protected nests showed greater reproductive success as well (Barber et al. 2010). Nest abandonment can often be a result of the mortality of an incubating adult, and in some cases predators become attracted to exclosures once they learn there is a food source within the fencing. Predators have been documented to target multiple nests within a short time frame, often referred to as “episodic” predation, once they learn to associate exclosures with food (Murphy et al. 2003a, Neuman et al. 2004, Hardy and Colwell 2008). Research conducted on lake beaches in Alberta, Saskatchewan, North Dakota, and Montana found that 5% of Piping Plover nests monitored with predator exclosures documented an adult mortality event, with most predation occurring in 2-10 day episodes, likely from raptors. In contrast, no unprotected nests experienced any adult mortality in the same study. (Murphy et al 2003a).

Though predator exclusion is one of the most widely used methods for increasing ground-nesting bird nest success (Gibbons et al. 2007), predator exclosures have only minimally been used and studied with Wilson’s Plovers (e.g., DeRose-Wilson et al. 2013), a migratory coastal breeding shorebird that is facing threats on its breeding grounds, such as predation, habitat degradation and human disturbance. This species nests solely in coastal beach habitats, and unlike other plover species, does not have any inland breeding populations (Corbat and Bergstrom 2000). Its range has contracted over the last century, and now it is no longer found breeding north of Virginia (Zdravkovic 2013). As a result, the species is listed on the U.S. Shorebird Conservation Plan as a “Species of High Concern (Category 4)” (Brown et al. 2001). Though Wilson’s Plovers have no federal protection, several states have designated the species for protection (Corbat and Bergstrom 2000). In Georgia, Wilson’s Plovers are listed as Threatened, and only 300 nesting pairs were estimated to occur in the state in 2010 (Sterling 2017). One of the severest threats to Wilson’s Plovers in Georgia is predation by wild, feral, and domesticated animals (GADNR 2010).

We conducted an investigation of the effects of predator exclosures on Wilson’s Plover nesting productivity at Little St. Simons Island, GA, USA. Previous research at this site indicates predation is a leading cause of Wilson's Plover nest failure (Sterling 2017). Our objectives were to estimate nest success of nests treated with predator exclosures and unexclosed (control) nests, monitor predator activity around exclosures, and estimate chick survivorship. We predicted nests with exclosures would have a higher nest success than untreated nests, more chicks would hatch from exclosed nests, and there would be no significant difference in chick survivorship between treatments. Additionally, we were interested in the effect of predator exclosures on Wilson's Plover population growth. We estimated the finite rate of increase (λ) for the Atlantic Coast population with and without the implementation of predator exclosures to see if this management technique alone could have an impact on the population.

STUDY AREA

Little St. Simons Island (31.25889, -81.28667, Glynn County, GA, USA) is a privately-owned barrier island that is protected as a nature reserve (Figure 3.1). The island is only accessible by boat, and as a result, is minimally disturbed by human activities. Little St. Simons Island is approximately 4,450 hectares and has roughly 11.25 km of beachfront shoreline. The beach dune system is comprised of sandspur (*Cenchrus tribuloides*), salt hay grass (*Spartina patens*), sea oats (*Uniola paniculata*), white-topped sedge (*Rhynchospora colorata*), sea purslane (*Sesuvium portulacastrum*), sea rocket (*Cakile edentula*), silver-leaf croton (*Croton punctatus*), sea pink (*Sabatia stellaris*), beach morning-glory (*Ipomoea imperati*), railroad vine (*Ipomoea pes-caprae*), and wax myrtle (*Morella cerifera*) typically acting as a barrier between dunes and later successional habitat. The Altamaha River empties into the Atlantic Ocean just north of Little St. Simons Island, and the river deposits sediment and nutrients that benefit breeding, wintering, and migrating shorebirds. Little St. Simons Island's rapidly accreting shoreline and intact dune system provides excellent habitat for beach-nesting birds, such as Wilson's Plovers, American

Oystercatchers (*Haematopus palliates*), and Least Terns *(Sternula antillarum*) (Schneider at al. 2010). As a result, Little St. Simons Island, as part of the Georgia Barrier Islands, was recently designated as a "Landscape of Hemispheric Importance" for numerous migratory shorebirds under the Western Hemisphere Shorebird Reserve Network (WHSRN 2017).

Approximately 9.5 km of Little St. Simon's Island coastline was surveyed for this study, which included the entire stretch of beach between the mouth of Mosquito Creek and the Altamaha River, and the section of beach west of Sancho Panza Creek. The beach was sectioned off into seven separate beach units based on anecdotal observations of paired breeding Wilson's Plover concentrations (Figure 3.2). Beach units served as spatial blocks to facilitate interspersion of exclosure treatments and the logistical need to work in sections rather than the entire beach for daily research activities.

FIELD METHODS

Nest Searching

Each unit of beach was surveyed by bike and/or foot every 1-3 days between mid-March and late July for new Wilson's Plover nests. All suitable nesting habitat was systemically searched with 1-2 people. When a new nest was found, the date, GPS coordinates, number of eggs, age of nest, number of adults present, and if banded, adult band combinations were recorded. Few adult birds were banded, so all renesting attempts were documented as new nests because pairs could not be uniquely identified. When a nest was found with a full clutch (i.e., three-egg nest, or one or two-egg nest after two nest checks), eggs were floated in water and compared to Bergstrom's (1982) egg development chart to determine nest age and estimated hatch day. After floating, eggs were placed back in the nest cup in the exact position they were found.

Exclosure Design and Deployment

The standardized exclosure design and methods recommended for the protection of Atlantic Coast Piping Plover nests were utilized for this project (USFWS 1996). A 2-4-person team assembled exclosures, and the entire set-up process had to be completed in under 20 minutes from the time the adult stopped incubating and departed the nest. Predator exclosures were set-up around the nest site in the morning and late evening hours to avoid overexposing the eggs to weather elements. Predator exclosures consisted of a 10-foot in diameter, circular 2x4 inch welded wire fence that was supported by 5 wooden posts (Figure 3.3). Exclosures were buried 8 inches into the substrate, and were 3 feet 4 inches above ground. The nest was directly in the center of the exclosure, so there was always at least 5 feet of space between the nest and fencing. A mesh net with holes less than 3/4 inches in size was attached to the top of the exclosure with 8 inch zip-ties. Zip-ties were affixed to the exclosure so the ends pointed upward to reduce perching by crows and grackles.

A trail camera was positioned to face either north or south to avoid direct sun glare, far enough away so the entire exclosure was visible on the images, and if possible, on a small mound to elevate the camera off of the ground for better infrared images and to avoid flooding. Once the exclosure was set up around the nest, the surrounding area was smoothed with a rake to remove signs of disturbance. Afterwards, everyone distanced themselves from the nest and waited for an adult to return to incubate the eggs. If neither parent returned to incubate within 1 hour, then it was assumed that they rejected the exclosure and it was immediately removed. The amount of time it took for a parent to return and incubate the nest was recorded.

The decision whether a nest was suitable for an exclosure was based on expert opinion. Nests that were located on relatively flat ground, without too much vegetation were able to be exclosed. Nests unsuitable for an exclosure were not included in this study, but continued to be monitored. Only nests with full 2 or 3-egg clutches were assigned a treatment. In 2016, predator exclosures were randomly assigned to nests within the first three days of egg development in separate beach units. This deployment method ensured that exclosure observation time was maximized. Nests not assigned a predator exclosure were monitored as control nests, including any nest that was found further along than 3 days in development. In 2017, the deployment strategy was modified for a systematic and balanced design. Every other suitable nest between 1 and 20 days developed was assigned a treatment. Since the exclosure set-up process was laborious and time-consuming, we prioritized younger nests to minimize effort and increase the exposure period for nests.

The exclosure and trail camera were removed once the adults moved the chicks away from the original nest site or if the nest failed. Removal occurred at the earliest possibility to minimize predators habituating to the exclosure or utilizing fencing as a perch. The removal process was done as quickly as possible to minimize disturbance to nearby nesting birds.

Nest Monitoring

Unexclosed nests and nests with predator exclosures were visually checked every 1-3 days until the nest either hatched or failed. If crows or grackles were in the vicinity of a nest being checked, then researchers waited until the birds left the area before approaching the nest. Exclosures were checked during nest monitoring to ensure there were no obstructions or buildup of sand around the fencing that may block incubating adults from accessing their nest. During every nest check the surrounding area was visually searched for signs of predators, and any tracks, ghost crab (*Ocypode quadrata*) burrows, or scat that was found within 10 meters of the nest was documented. A nest was classified as either successful or failed. A successful nest fate was assigned when at least one egg hatched. The cause of failure was determined for failed nests, if possible, by examining the surrounding area for signs of flooding, human disturbance, predator tracks and scat, and egg shells. When the cause of failure was unable to be determined then “unknown” was recorded. If either predator signs or disturbance were near the nest but were unidentifiable to a species or a nest failed not a result of flooding, then the cause of failure was documented as “unknown predation”. Trail cameras and data were checked every 5-7 days to change SD memory cards, monitor for predator activity, and to ensure the cameras were properly functioning.

Chick Survivorship

Wilson’s Plover chicks can walk within a few hours of hatching (Bergstrom 1988a), so chicks were color-banded prior to leaving the nest cup. Each individual young received a unique color combination on their lower legs (tarsus). Chicks found within exclosures were not moved outside of the exclosures because we wanted to determine if predators depredated chicks as they exited fencing. Any signs of disturbance (i.e., foot prints) were smoothed with sand before leaving the nest site area.

Resighting surveys occurred twice a week between May and August to relocate banded broods and determine fledging success. During these surveys, the entire beach and adjacent high marsh were covered by bike and/or foot with a spotting scope. Typically, an adult was spotted first then the surrounding area was scanned for young. When a banded chick was spotted, its band combinations, GPS coordinates, distance (meters) and cardinal direction from the observer, habitat, and behavior were recorded. Resighting young was done from a distance away (up to 100 m) as to not disturb the brood. If a brood was disturbed, researchers distanced themselves far enough away so the chicks emerged from hiding. When young approached fledgling age, they were monitored for their first flight. Following Sterling (2017), any young located after 36 days were assumed to be fledged.

Habitat Surveys

Surveys were conducted at nest sites once a nest hatched and the chicks were moved away from the area, or once the nest failed. For exclosed nests, these data were collected before the exclosure was removed to avoid destroying ghost crab burrows. Whether the nest was located in vegetation and the number of ghost crab burrows in a 5-foot radius around the original nest site were documented. The habitat type was recorded within a 20-meter radius around the original nest site. Similar to Sterling's (2017) habitat classification protocol, nests were assigned one of 14 habitat classifications (Table 3.1). Habitat types were also sectioned into front or back beach categories with the primary dune ridge acting as a boundary between sections. For habitats which could be classified as either front or back beach (e.g., beach pond and fiddler crab salt pan), the researcher subjectively determined the section of beach for the particular habitat. Research activities were not executed if temperatures were greater than 38º C, precipitation was falling, or if winds exceeded 32 kph.

ANALYTICAL METHODS

Nest Success

A logistic exposure model was used to calculate the daily survival rate (DSR) of nests (Rotella et al. 2004, Shaffer 2004) in Program R 3.4.3 (R Development Core Team 2017). Habitat type, section of beach (front or back), beach unit, highest tidal water level between nest checks, nest located in or out vegetation, number of ghost crab burrows, treatment, nest age, and year were used as covariates in the model (Table 3.2). A total of 45 models was run including a global model incorporating all of the parameters and a null model (Table 3.3). The Akaike's

Information Criterion corrected for small sample size (AICc) ranked models for nest survival analyses (Burnham and Anderson 2002). Models under 4 Δ AICc were model averaged to estimate parameters. Top AICc model results are presented with the null model for comparison.

Predator Activity

The mean, standard deviation, minimum and maximum number of ghost crab burrows in a 5-foot radius around the nest site was computed for each treatment and means were compared with a two-sample t-test. The distance (meters) from unexclosed nests to the closest exclosure was calculated in ArcMap 10.4.1 (ESRI 2017). Distance was input as a covariate in a logistic exposure model containing data from only unexclosed nests to determine if exclosures caused an increase in predation to nearby unexclosed nests.

Incubation Times

The mean, standard deviation, standard error, and minimum and maximum incubation time (days) were analyzed for each treatment and year. We used a randomized blocked analysis of variance (ANOVA) to test for differences in incubation times with beach units serving as a spatial block.

Chick Survivorship and Fledge Rates

The number of chicks hatched per nesting attempt was estimated for each treatment. The number of fledglings produced per nesting attempt was assessed by multiplying the number of chicks hatched per nesting attempt by the overall survival probability for each treatment. Determining an exact estimate for number of nesting pairs within each treatment was unattainable because so few adults were banded at the study area.

A Cormack-Jolly-Seber model was used in the R version 3.4.3 (R Development Core Team 2017) package RMark (Laake 2013, White and Burnham 1999) to estimate apparent survival (φ) and detection probability (*p*) . The quasi-likelihood Akaike's Information Criterion corrected for small sample size (QAICc) ranked models for survival analyses (Burnham and Anderson 2002).

Survival rates were estimated using six encounter intervals up to 36 days that were each six days long, and assumed chicks were capable of flight after 36 days (Sterling 2017). Survival and detection varied by time. Also, survival varied by using year and treatment as groups, and detection varied by year. Models also incorporated the influence of hatch date and height of highest tide on survival rates as individual covariates for each chick (Table 3.4). A total of 20 models was built, including the intercept-only model and a global model with the additive effects of all the variables incorporated to estimate the influence of weather and predation risk on chick survival. Model covariates whose 95% confidence limits did not include zero were considered to be statistically significant in our results. Finally, the overall survival rate was calculated for the entire period from hatch until fledging from the best ranked model (Powell 2007).

Population Growth Rate

The finite rate of increase (λ lambda) was assessed using only the female portion of the Atlantic Coast Wilson's Plover population. We calculated lambda for three management scenarios: 100% nests exclosed, 50% nests exclosed, and 0% nests exclosed. We did an eigen analysis on a 2x2 stage-structured matrix to estimate λ with S_J*f and S_A*f on the first row and S_J and S_A on the second row, where S_J is the annual juvenile survival rate, S_A is the annual adult survival rate, and f is fecundity. Fecundity is the number of female chicks produced per nesting attempt (C_N) multiplied by the survival probability of unfledged chicks (S_C).

Survival estimates for Wilson's Plovers are limited or are unknown (Corbat and Bergstrom 2000). True adult and juvenile annual survival is unknown, so survival estimates for

Snowy Plovers, a close relative, was used for this study. The female adult survival estimate ($S_{A)}$ for Snowy Plovers is estimated to be 0.622 ± 0.015 (Méndez et al. 2018). Juvenile annual survival of Snowy Plovers ranges annually between 0.283 ± 0.028 and 0.575 ± 0.061 (Stenzel et al. 2007), so we averaged the estimates together ($S_J = 0.429$).

RESULTS

General

In total, 335 Wilson's Plover nests were found on Little St. Simons Island, 41 nests were monitored with exclosures, and 68 unexclosed nests were monitored as controls. In 2016, a total of 135 Wilson's Plover nests was located, and 18 exclosed and 41 control nests were monitored for this study. In 2017, a total of 200 Wilson's Plover nests was found, and 23 exclosed and 27 control nests were monitored. Incomplete clutches and nests that were incapable of being exclosed were not included in analysis.

The frequency of nest checks was 2.35 ± 1.21 days in 2016, and 2.09 ± 0.98 days in 2017. The treatment and block effects on incubation time were not significant. In 2016, the incubation time was 29.82 ± 1.25 (SE = 0.38, min = 28, max = 32) days for exclosed nests and 30.55 ± 2.56 (SE = 0.57, min = 27, max = 35) days for unexclosed nests. In 2017, the incubation time was 30.58 ± 1.68 (SE = 0.38, min = 27, max = 34) days for exclosed nests and 30.50 ± 1.29 (SE = 0.65, min = 29, max = 32) days for unexclosed nests.

Predator Exclosures

Fifty-three exclosures were deployed in total for this study. In 2016, 19 exclosures were deployed, and one was rejected when the adults did not return to incubate the nest (95% acceptance rate). Eleven out of 34 exclosures deployed in 2017 were rejected (68% acceptance rate).

The average amount of time spent setting up exclosures at nest sites once a bird stopped incubating was 16.05 ± 3.22 minutes. The minimum and maximum set up times were 8 and 25 minutes, respectively. The set-up time exceeded 20 minutes for 4 exclosure deployments (8% of total exclosures). For 3 exclosures only two people were constructing the exclosure when the time limit was exceeded. A plover returned to incubate in every exclosure in this situation. When an adult was seen returning to the nest in an open area (*n* = 15), the average return time was 7.53 ± 7.82 minutes. The shortest and longest time for a plover to return and incubate was 1.5 and 28 minutes, respectively. A team of 3 people set up 38 exclosures (72%), 2 people set up 9 exclosures (17%), 4 people set up 5 exclosures (9%), and 5 people set up 1 exclosure (2%).

We did not observe any behavioral change among any adults incubating nests within predator exclosures. Adults and chicks were observed traveling through fencing without issue, and adults slightly lowered their head as they passed through the 4x2" spacing. Incubating birds departed the exclosure by foot when approached by researchers, but there was one occurrence of an adult flying into the netting in 2016. During this event, two researchers walked up to a hatching nest within an exclosure and their approach was moderately blocked by vegetation to the incubating adult. The adult flew up into the net twice before exiting by foot and appeared uninjured. The two chicks and one egg in the nest cup were unharmed.

Non-predatory species observed perching or roosting on exclosures were Least Tern (*Sternula antillarum*) and Common Nighthawk (*Chordeiles minor*) (Figure 3.4). During these instances, an adult was observed incubating via direct observations or trail camera footage. There was one occurrence of a Least Tern within an exclosure. The tern was within the exclosure fencing when researchers flushed the bird, which caused it to fly and repeatedly hit the net.

Researchers immediately backed off, and the tern stopped flying and exited the exclosure by foot. No eggs were harmed during this event.

Nest Failures and Predator Activity

A total of 11 of 41 (27%) exclosed nests and 44 of 68 (65%) control nests failed in this study. In 2016, 21 of 41 (51%) control nests failed, and 7 of 18 (39%) exclosed nests failed. In 2017, 23 of 27 (85%) control nests failed, and 4 of 23 (17%) exclosed nests failed. In 2016, exclosed nests failed to ghost crab predation (n = 3), tidal wash over (n = 3), and abandonment (n = 1), and unexclosed nests failed to tidal wash over (n = 8), unknown predation (n = 5), raccoon predation (n = 3), coyote predation (n = 3), avian predation (n = 1), and armadillo predation (n = 1) (Figure 3.5). In 2017, exclosed nests failed to ghost crab predation (n = 3) and tidal wash over (n = 1), and unexclosed nests failed to raccoon predation (n = 10), unknown predation (n = 9), avian predation (n = 2), ghost crab predation (n = 1), and blown over with sand from strong winds unrelated to abandonment (n = 1) (Figures 3.6, 3.7).

Since trail cameras were only placed at nests with exclosures, a comparison of predator activity between treatments is unattainable. However, there was an increase in Fish Crow and raccoon visitation to exclosures during the second year of the study. In 2016, raccoons did not attempt to enter exclosures. Fish Crows were captured on trail camera images perching on and circling three different exclosures. During this time, the adults were off the nest, leaving the eggs exposed to weather elements. In 2017, raccoons were observed circling and/or digging at least once during incubation at 18/23 (78%) of exclosures. Racoons were able to dig approximately 4 inches into the ground, but were unable to enter exclosures. No direct adult or chick mortality was captured on trail cameras, however, one freshly hatched chick that appeared barely alive was found within an exclosure (Figure 3.8). Researchers approached the exclosure for chick banding to find raccoon tracks circling and reaching into the exclosure. The weak chick was covered in a thin layer of sand near the spot disturbed from the raccoon reaching into the exclosure. The parents were not in the vicinity, and the thin layer of sand on the chick indicated they had not returned to brood the chick recently. The chick was banded and placed in the nest cup with the two remaining unhatched eggs. The remaining two eggs hatched within 48 hours of the incident, and one adult was in the area while the chicks were banded. The first chick was never sighted again, and likely died.

Ghost crabs were the only predator to depredate nests in an exclosed nest in either year. Ghost crab predation events were captured on trail cameras during both the day and night, and it typically took several hours for the crab to remove all eggs from the nest. There were significantly more ghost crab burrows at nests with exclosures than nests without exclosures in 2016 ($P = 0.042$) and 2017 ($P = 0.002$). In 2016, there was an average of 1.56 ± 1.76 (min = 0, max = 7) burrows at exclosed nests and 0.56 ± 1.34 (min = 0, max= 5) burrows at unexclosed nests. Approximately, 72% of all exclosed nests and 29% of unexclosed nests had at least 1 ghost crab burrow within a 5-foot nest radius. The data were unbalanced in 2016 since there were 41 control and 18 exclosed nests, and the few control nests that did have ghost crab activity had multiple burrows. In 2017, there was an average of 1.78 ± 1.48 (min = 0, max = 5) burrows at exclosed nests and 0.63 ± 0.69 (min = 0, max = 2) burrows at unexclosed nests. An estimated 52% and 88% of unexclosed and exclosed nests, respectively, had at least 1 ghost crab burrow within close vicinity.

The closest unexclosed nest to an active exclosure between all years was 6.13 meters. Despite the close proximately between some exclosed and unexclosed nests, it appears that exclosures did not influence predation rates on unexclosed nests. There was no significant effect of exclosures increasing failure rates on nearby unexclosed nests.

Nest Success

Every top model, except one, included the effect of treatment throughout all years (Table 3.5). In 2016, the effect of treatment and tide model held 0.54 of the weight, and was the top model. In 2017, the top model included treatment and beach unit, which held 0.38 of the weight, and the second most important model had the parameters treatment, beach unit, and number of ghost crab burrows, which had 0.27 of the weight. This suggests that there was a spatial block effect in 2017. When both years were combined, the top model included treatment and tide with 0.30 of the weight. Beta (β) estimates were derived from the top model (Table 3.6). The effect of exclosures ($\beta = 1.65$, SE = 0.37) had the greatest impact, which was positive, on nest survival indicating that the treatment was effective at limiting nest predation. The survival of nests was negatively correlated with high tide ($\beta = -0.32$, SE = 0.15) since nests could fail from tidal overwash.

Exclosed nests had a higher daily survival rate (DSR) than unexclosed nests in both 2016 and 2017 (Figure 3.9). In 2016, 21 control nests failed and 20 nests hatched, and 7 exclosed nests failed and 11 hatched. In 2017, 23 control nests failed and 4 nests hatched, and 4 exclosed nests failed and 19 nests hatched (Figure 3.10). In 2016, there were 419 nest checks, and the DSR was 0.984 (SE = 0.446) and 0.959 (SE = 0.227) for exclosed and unexclosed nests, respectively. When the DSR was raised to the 25th power for a 25-day incubation period, exclosed and unexclosed nests had a 66% and 35% total nest success rate, respectively. In 2017, there were 469 nest checks, and the DSR was 0.993 (SE = 0.50) and 0.931 (SE = 0.219) for exclosed and unexclosed nests. The overall nest success rate was 84% for exclosed nests, and 17% for unexclosed nests. The treatment effect of predator exclosures was significant in 2016 ($P = 0.032$) and 2017 ($P < 0.0001$). There was no significant difference in treatments between years.

Chick Survivorship and Fledge Rates

Significantly more chicks hatched per nesting attempt from nests with predator exclosures than unexclosed nests in 2017 ($P < 0.0001$), but not in 2016 (Figure 3.11). Among exclosed and unexclosed treatments in 2016, 1.72 ± 1.45 and 1.06 ± 1.37 chicks hatched per nesting attempt, respectively. In 2017, 2.26 ± 1.18 chicks hatched per nesting attempt for exclosed nests, and 0.41 ± 1.01 chicks hatched per nesting attempt for unexclosed nests. More young fledged from breeding attempts that had a nest exclosure than from pairs that had unexclosed nests, though this was only significant in 2017 ($P < 0.0001$) (Figure 3.12). In 2016, 0.75 ± 0.63 and 0.48 ± 0.62 fledglings per nesting attempt were produced among the exclosed and unexclosed treatment groups, respectively. In 2017, 0.35 ± 0.18 young fledged per nesting attempt among the exclosure treatment group and 0.07 ± 0.17 young fledged per nesting attempt among the unexclosed treatment group.

The top QAICc model included all of the model parameters for survival (φ) and detection (p), and had approximately 95% of the total weight (w_i) (Table 3.7). Beta (β) estimates were derived from the top model (Tables 3.8, 3.9). Time was the only parameter that had a positive influence on survival ($\beta = 0.458$, SE = 0.181); the probability of survival increased with each time interval or as the chick aged (Figures 3.13, 3.14). The day of hatch had a negative effect on survival ($\beta = -0.684$, SE = 0.176), so chicks hatched later in the breeding season were less likely to survive. The year 2017 ($\beta = -1.090$, SE = 0.362) was negatively associated with chick survival. The survival of chicks hatched from different nest treatments within years was not significantly different. The parameter time ($\beta = 0.337$, SE = 0.116) also had a positive association with detection probability. This result likely indicates that observers improved their ability to relocate banded chicks as the breeding season progressed (Figure 3.15). Detection probability was also negatively associated with observer. Overall, the likelihood of detection was 0.362 (SE = 0.064) in 2016 and 0.620 (SE = 0.062) in 2017.

Chick survival was higher in 2016 than 2017, but the difference was not significant (Figure 3.16). Estimates for overall survival was 0.452 (SE = 0.122) and 0.388 (SE = 0.121) in 2016, and 0.115 (SE = 0.105) and 0.098 (SE = 0.090) in 2017 for chicks hatched from unexclosed and exclosed nests, respectively.

Population Growth Rate

Fecundity was estimated using results from this study. We averaged chick survival estimates since the survival probability did not significantly differ between treatments ($S_C = 0.302$). We assumed an equal sex ratio in young, so the number of female chicks produced per nesting attempt for each scenario (100%, 50%, and 0% nests exclosed in regional population) was 0.995 ± 0.658, 0.6805 ± 0.626, and 0.366 ± 0.595, respectively. Therefore, $f = 0.300$, 0.205, and 0.111 for the 100%, 50%, and 0% nests exclosed scenarios.

The finite rate of increase (λ) for the 100%, 50%, and 0% nests exclosed management scenarios was 0.751, 0.710, and 0.669. Since $\lambda < 1$, the Atlantic Coast population of Wilson's Plovers is likely in decline. If f and S_J are held constant, adult survival needs to be increased to 0.872, 0.912, and 0.953 in the 100%, 50%, and 0% nests exclosed scenarios, respectively, to attain a $\lambda \geq 1$. If S_A and S_J are held constant, fecundity needs to be increased to 0.889 to attain a $\lambda \geq 1$.

DICUSSION

The results from this study demonstrate that predator exclosures are effective at increasing Wilson's Plover nest success. Though some research reports predator exclosures as having no effect on shorebird nest success (Mabee and Estelle 2000), the majority of predator exclusion studies focused on ground-nesting birds indicate that exclosures decrease nest predation (Smith et al. 2011). Among shorebirds, predator exclosures increased nest success of Piping Plovers (Melvin et al. 1992, Maslo and Lockwood 2009, Doherty and Heath 2011) and Snowy Plovers (Neuman et al. 2004, Hardy and Colwell 2008, Pearson et al. 2016). DeRose-Wilson et al. (2013) also found exclosed Wilson's Plover nests had a higher daily survival rate than nests without exclosures, but sample size was limited to 17.

High tides also played an important role in the survival of nests, especially in 2016. Tides were negatively associated with nest survival and were the second most important factor, behind exclosure treatment, as a model predictor. These nest failures could be avoided in future applications by specifically targeting nests further from the tide line for exclosures.

Although more chicks hatched per breeding attempt from nests with predator exclosures, fledge rates were similar between treatments in 2016. The number of young fledged over both years averaged 0.41 ± 0.40 young fledged per breeding attempt among the exclosed treatment, and 0.27 ± 0.39 young fledged per breeding attempt among the control group. These results are similar to Hardy and Colwell's (2008) predator exclusion study with Snowy Plovers which also found a higher nest success among exclosed nests and unexclosed nests, but no significant increase in fledge success (Hardy and Colwell 2008). As predicted, we found chick survival did not significantly differ between nest treatments. Predator exclosures are only effective at deterring predators during the incubation phase for precocial chicks. Techniques to reduce predator disturbance throughout the breeding season (i.e., lethal removal) may be needed to increase fledge rates, and thus, productivity.

Contrary to previous reports for other species (Barber et al. 2010), we did not find a higher abandonment rate among nests with predator exclosures. In this study, only one nest abandonment was documented at a predator exclosure throughout all years. No unexclosed nests were abandoned. We believe one abandonment at an exclosed nest over two years is minimal, and no reason for concern. No adult mortality was observed either visually or through trail cameras at any exclosed nests, including the abandoned nest. However, predator activity at exclosures was more frequent and disruptive in 2017 than 2016. Raccoons were observed circling and attempting to dig under exclosures in the second year of the study, but these behaviors were not seen in 2016. This delayed attraction to exclosures possibly indicates a learned behavior by predators that could result in adult mortality at exclosures in subsequent years. Other studies report depredation of nests and/or adults by a variety of mammalian and avian predators, but also used a smaller, 1-m diameter cage (Nol and Brooks 1982, Johnson and Oring 2002, Murphy et al. 2003b, Niehaus et al. 2004). In some cases, the smaller exclosure size could allow predators to reach through the fencing to depredate nests (Nol and Brooks 1982). A justification for the absence of adult mortality from this study could be there is minimal high vegetation near suitable Wilson’s Plover breeding habitat on Little St. Simons Island for raptors to perch in. Murphy et al. (2003b) did not observe any adult mortality, even at small cages, at a breeding area lacking trees, which suggests raptors were responsible for high adult predation rates elsewhere.

Although predator exclosures successfully protected Wilson’s Plover nests from mammalian and avian predation, an additional predator capable of entering exclosures and responsible for depredation of protected nests was the ghost crab. The Atlantic ghost crab is one of the largest invertebrates on ocean beaches and occupies beaches of the Georgia coast (Lucrezi and Schlacher 2014). They have been documented to feed upon more than 40 taxa of prey species (Lucrezi and Schlacher 2014). We did not visually observe direct predation by ghost crabs during this study, however, crabs were captured on trail camera images preying on eggs within exclosures. Ghost crabs create complex burrows in the sand for protection from predators, weather elements, and desiccation (Byerly and Crowe 1998). There were significantly more ghost crab burrows at nests with exclosures than unexclosed nests in this study, which causes some concern. In North Carolina, the survival of Piping Plover nests was lower when ghost crabs were present in the vicinity, and ghost crabs were responsible for 53% of the 17 exclosed nest failures (Kwon et al. 2018). In Florida, ghost crabs were the most common predator of Snowy Plover eggs, accounting for 64% of depredation events. Snowy Plover nests were more likely to hatch in areas further away from ghost crab burrows (Pruner 2010). Wolcott and Wolcott (1999) suggested shorebirds view ghost crabs as a threat since plovers were observed exhibiting defensive behavior towards them. Direct ghost crab predation was not observed during their study, but eggs and young could be indirectly negatively affected when a threat distracts parents. We observed parents exhibiting a broken wing display to ghost crabs within and outside the predator exclosures on trail camera images and during chick resighting surveys. Despite the negative effect of ghost crabs, nest success was still significantly higher among nests in the exclosed treatment.

More predator exclosures were rejected in 2017 (*n* = 11, 32%) than 2016 (*n* = 1, 5%) when an adult did not resume incubation within the allotted time. The exclosure design and deployment methods were identical among years, but 2017 exclosures were rejected consistently throughout the breeding season and across habitats. Only full clutches were exclosed in this study to maximize the acceptance rate. Melvin et al. (1992) deployed predator exclosures around two incomplete Piping Plover clutches, and both pairs accepted the exclosure and laid the final egg within 24 hours. Also, 2 out of 31 exclosures (6%) deployed had a pair that did not return to incubate the nest in that study. One of the pairs which rejected an exclosure nested at a site with minimal human disturbance, and appeared less habituated to anthropogenic activities. Little St. Simons Island is remote, privately-owned, and very minimally disturbed by human activities, however the level of disturbance did not change between years. Few adult birds were banded on Little St. Simons Island, so pairs were not uniquely identified. It is possible that individuals that did not accept the exclosure in 2017 had a predator exclosure deployed at their nest in both years, and were less tolerant the second year.

A major question remains as to whether techniques such as predator exclosures aimed at increasing nest success actually have an effect on Wilson’s Plover population numbers. More research is needed regarding Wilson’s Plover demography to determine if this management technique is successful at stabilizing or increasing the population. Wilson’s Plover lifespan, and juvenile and adult survival probabilities are unknown (Corbat and Bergstrom 2000), and only estimates for apparent survival exist (DeRose-Wilson et al. 2013). On the Atlantic Coast, a scarce number of Wilson’s Plovers are uniquely banded, and a greater effort should be put forth to color-band individuals. Banding is also required to estimate seasonal fecundity and related parameters such as time between clutches. As a preliminary estimate, if every single nest in the Atlantic Coast population was protected with a predator exclosure then the growth rate would still be in decline ($\lambda = 0.751$), although this estimate did not take renesting into account.

Additional predator management and lethal control may be needed help stabilize or increase the growth rate.

MANAGEMENT IMPLICATIONS

Protecting Wilson's Plover nests with predator exclosures can increase daily nest survival. Before implementing predator exclosures at a breeding site, an understanding of the local predator community is necessary for survival of eggs, young, and incubating adults. Alternating years in which exclosures are deployed may increase the acceptance rate when adults return to incubate. Exclosures are likely more effective at breeding sites during years that will experience low tides and high predation. To maximize time and resources, managers should try to predict tidal amplitude and predation rates prior to the breeding season, and target nests further away from the tide line for exclosures. Predator exclosures are only effective for the protection of eggs, and other predator management techniques should be employed for greater chick survival and productivity.

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TABLES

Table 3.1: Beach Habitat Classification. The description and location of different habitats on Little St. Simons Island in which Wilson's Plovers could nest, forage, or care for broods.

Section of Beach	**Habitat Type**	**Description**
Front	Active Dunes	Active, building dunes, with plants such as beach elder, sea oats and beach croton. Usually primary dune ridge, just behind wrack line. Can be semi permanent and well developed.
	Open Beach	Open, non-vegetated sand above the tideline, but not beyond primary dunes.
	Open Beach Low Tide	Open beach below the high tide line.
	Overwash Beach	Open beach or overwash fan that is frequently washed over by extreme tidal events. May be vegetated with high salt tolerant species and be scoured by wind. Early successional.
Front/Back	Beach Pond	A permanent or semi-permanent body of water, usually brackish, and can be connected to the ocean on the front side of the beach, or the marsh on the backside of the beach.
	Fiddler Crab Salt Pan	Open muddy areas with limited vegetation, dominated by fiddler crabs. Frequently overwashed on highest tides.
Back	Dense *Spartina patens*	Monoculture areas of *Spartina patens* .
	Inactive Dunes	Well established dunes, vegetated, usually at least one or two primary dune ridges west of the ocean.
	Interdune Meadow	Low, vegetated areas, generally dominated by low growing plants, grasses and forbs.
	Interdune Swale	Low areas, between dunes, not heavily vegetated. Precursor to interdune meadow.
	Marsh	Marsh dominated by vegetation such as *Spartina alterniflora* and *Juncus roemerianus* .
	Open Sand	Open sand landward of the first primary dunes. Non-vegetated.
	Salicornia	Patches of *Salicornia sp* . and Sea Purslane. More vegetated than fiddler crab salt pans.
	Wax Myrtle	Medium to tall shrubs of both *Morella cerifera* and *Baccharis halimifolia* .

Table 3.2: Nest Success Covariates. Descriptions of the parameters used in the logistic exposure model to assess the daily survival rate of Wilson's Plover nests.

Parameter	**Type**	**Description**
Age	Categorical	Age of nest when initially found
Crab_Holes	Categorical	Number of ghost crab burrows within a 5-foot radius of the nest site
Habitat	Categorical	Type of habitat 20-meters around nest site, see Habitat Classification table
Nest_in_veg	Binomial	Assigned a "1" if the nest was located in vegetation, and "0" if the nest was open
Section	Categorical	Either front or back beach, see Habitat Classification table
Tide	Continuous	Amplitude of the highest tide between nest checks
Treatment	Categorical	The nest treatment, either control or exclosed
Unit	Categorical	The beach unit in which nests were spatially blocked, see Beach Unit figure
Years	Categorical	Year in which nest was active, either 2016 or 2017

Table 3.3: Nest Success Models. A complete list of the 45 models run in a logistic exposure model to determine the daily survival rate of Wilson's Plover nests.

Models	
1	Crab_Holes+Nest_in_veg
2	Crab_Holes+Age
3	Crab_Holes+Section+Nest_in_veg
4	Crab_Holes+Habitat+Nest_in_veg
5	Crab_Holes+Section
6	Crab_Holes+Habitat
7	Unit+Section
8	Unit+Habitat
9	Unit+Habitat+Nest_in_veg
10	Unit+Section+Nest_in_veg
11	Unit+Crab_Holes
12	Habitat+Tide
13	Section+Tide
14	Crab_Holes
15	Habitat
16	Nest_in_veg
17	Unit
18	Section
19	Age
20	Tide
21	Years
22	Treatment+Crab_Holes+Nest_in_veg
23	Treatment+Crab_Holes+Age
24	Treatment+Crab_Holes+Section+Nest_in_veg
25	Treatment+Crab_Holes+Habitat+Nest_in_veg
26	Treatment+Crab_Holes+Section
27	Treatment+Crab_Holes+Habitat
28	Treatment+Unit+Section
29	Treatment+Unit+Habitat
30	Treatment+Unit+Habitat+Nest_in_veg
31	Treatment+Unit+Section+Nest_in_veg
32	Treatment+Unit+Crab_Holes
33	Treatment+Habitat+Tide
34	Treatment+Section+Tide
35	Treatment+Crab_Holes
36	Treatment+Habitat
37	Treatment+Nest_in_veg
38	Treatment+Unit
39	Treatment+Section
40	Treatment+Age
41	Treatment+Tide
42	Treatment+Years
43	Treatment
global	Treatment+Crab_Holes+Habitat+Section+Unit+Age+Years+Nest_in_veg
null	1

Table 3.4: Chick Survival Covariates. Descriptions of the covariates used to assess the survival probability of Wilson’s Plover chicks.

Parameter	**Type**	**Description**
Phi(~hatch)	Categorical	Julian day for the hatch date of chicks
Phi(~hightide)	Categorical	Amplitude of the highest tide during the chick's pre-fledged stage
Phi(~Time)	Continuous	The continued progess of survival for each encounter interval
Phi(~treatment)	Categorical	The nest treatment that chicks hatched from, either control or exclosed
Phi(~year)	Categorical	Year in which chicks hatched, either 2016 or 2017
P(~obs)	Categorical	Observers were LGRD in 2016 and LGKT in 2017
P(~Time)	Continuous	The continued progess of dectection for each encounter interval

Table 3.5: Nest Survival Top $\mathrm{AIC_c}$ Models. The top $\mathrm{AIC_c}$ models under 4 $\Delta\mathrm{AIC_c}$ predicting nest daily survival rate for the 2016, 2017, and combined 2016 and 2017 breeding seasons. The null model is shown for comparison.

Year	**Model**	**K**	**AICc**	**ΔAICc**	**w_i**
2016	Treatment+Tide	3	235.513	0.000	0.538
	Treatment+Section+Tide	4	237.550	2.037	0.194
	Tide	2	238.575	3.062	0.116
	null	2	245.795	10.282	0.003
2017	Treatment+Unit	3	201.605	0.000	0.382
	Treatment+Unit+Crab_Holes	4	202.332	0.727	0.266
	Treatment+Unit+Section	4	203.625	2.020	0.139
	null	2	233.080	31.475	0.000
Combined	Treatment+Tide	3	447.429	0.000	0.300
	Treatment+Age	3	449.033	1.604	0.135
	Treatment+Section+Tide	4	449.086	1.657	0.131
	Treatment	2	450.236	2.806	0.074
	Treatment+Crab_Holes+Age	4	450.499	3.069	0.065
	Treatment+Unit	3	450.512	3.083	0.064
	null	2	476.846	29.417	0.000

Table 3.6: Nest Survival Beta (β) Estimates. Beta (β) estimates from the combined 2016 and 2017 top AIC_c model, which indicates that the treatment of exclosures positively influenced nest survival while high tides negatively impacted survival.

Coefficient	**Estimate**	**Std. Error**
TreatmentExclosure	1.57	0.344
Tide	-0.315	0.147

Table 3.7: Top AIC_c Chick Survival Models. Chick survival models ranked in order from lowest to highest ΔAIC_c. The global model ranked highest with approximately 96% of the model's weight.

Model	**K**	**AICc**	**ΔAICc**	**w_i**	**Deviance**
Phi(~hatch + hightide + treatment + year + Time)p(~obs + Time)	10	585.440	0.000	0.959	564.516
Phi(~hatch + hightide + treatment + year + Time)p(~obs)	9	592.588	7.143	0.027	573.831
Phi(~hatch + year)p(~Time)	5	595.324	9.880	0.007	585.076
Phi(~hatch + hightide + treatment + year + Time)p(~Time)	9	595.540	10.096	0.006	576.784
Phi(~hatch + hightide + treatment + year + Time)p(~1)	8	600.719	15.274	0.000	584.117
Phi(~hatch + year)p(~obs)	5	601.828	16.383	0.000	591.580
Phi(~hatch)p(~Time)	4	604.824	19.380	0.000	596.660
Phi(~hightide)p(~Time)	4	617.858	32.414	0.000	609.694
Phi(~hightide + year)p(~Time)	5	618.645	33.200	0.000	608.397
Phi(~hatch)p(~obs)	4	619.353	33.909	0.000	611.189
Phi(~year)p(~Time)	4	621.292	35.848	0.000	222.235
Phi(~year * treatment)p(~obs)	8	624.764	39.320	0.000	217.270
Phi(~year + treatment)p(~Time)	6	625.325	39.880	0.000	222.084
Phi(~year)p(~obs)	4	626.144	40.670	0.000	227.088
Phi(~treatment)p(~Time)	5	626.145	40.700	0.000	225.005
Phi(~hightide + year)p(~obs)	5	627.275	41.830	0.000	617.027
Phi(~year + treatment)p(~obs)	6	629.332	43.888	0.000	226.092
Phi(~hightide)p(~obs)	4	631.792	46.347	0.000	623.627
Phi(~1)p(~1)	2	637.874	52.430	0.000	242.933
Phi(~treatment)p(~obs)	5	638.216	52.772	0.000	237.076

Table 3.8: Chick Survival Beta (β) Estimates. Beta (β) estimates of the survival parameters from the top AIC_c model predicting chick survival.

Parameter	Estimate	SE
Phi:(Intercept)	1.062	0.384
Phi:hatch	-0.684	0.176
Phi:hightide	-0.031	0.153
Phi:treatmentExclosed	-0.065	0.351
Phi:treatmentNo	-0.278	0.415
Phi:year2017	-1.09	0.362
Phi:Time	0.458	0.181

Table 3.9: Detection Probability Beta (β) Estimates. Beta (β) estimates of the detection parameters from the top AIC_c model predicting chick survival.

Parameter	Estimate	SE
p:(Intercept)	-0.157	0.264
p:obsLGRD	-1.116	0.325
p:Time	0.337	0.113

FIGURES

Figure 3.1: Study Area. The study area, Little St. Simons Island, GA, is approximately 4,450 hectares with 11.25 km of beach-front coastline.

Figure 3.2: Beach Units. The different beach units and their corresponding Wilson's Plover nesting concentration on Little St. Simons Island acted as spatial blocks for the study.

Figure 3.3: Predator Exclosure Photograph. A predator exclosure set-up around a Wilson’s Plover nest. Exclosures were constructed from 2x4-inch welded wire fencing, 10-feet in diameter, and had a mesh net on top. The nest site needed to be relatively flat and with minimal vegetation for an exclosure to be suitable.

Figure 3.4: Nighthawk on Exclosure Photograph. A Common Nighthawk (*Chordeiles minor*) roosting on a predator exclosure while an undisturbed adult incubated the protected nest.

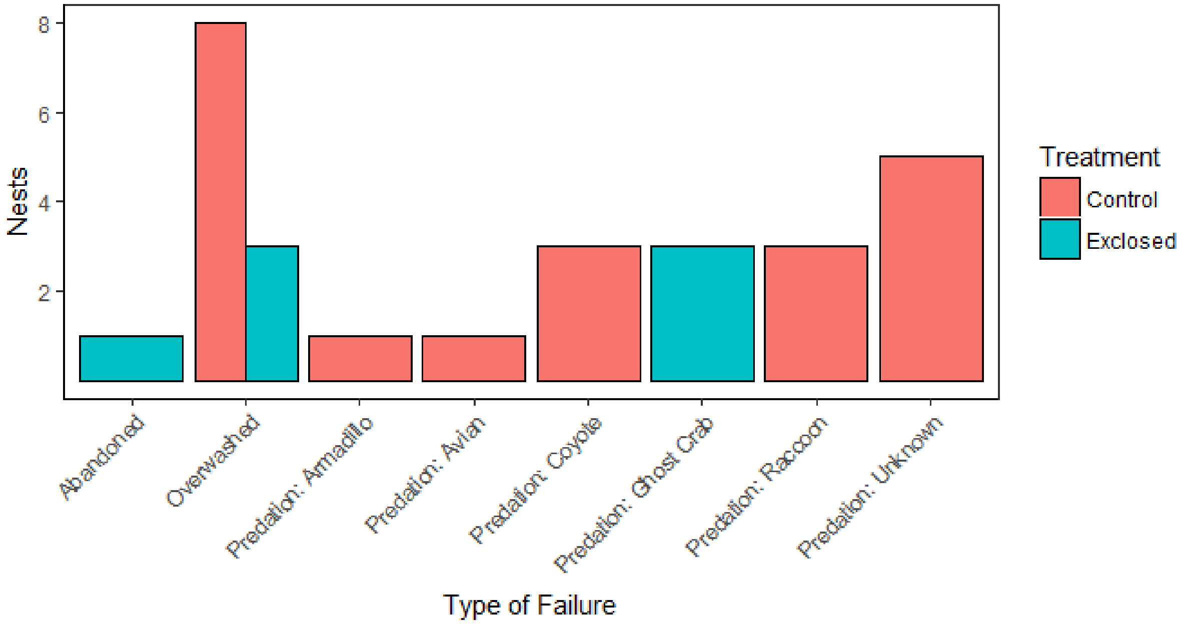

Figure 3.5: Nest Failures in 2016. The causes of nest failure among unexclosed and exclosed nests in 2016. Tidal overwash was a top cause of nest failure for both treatments.

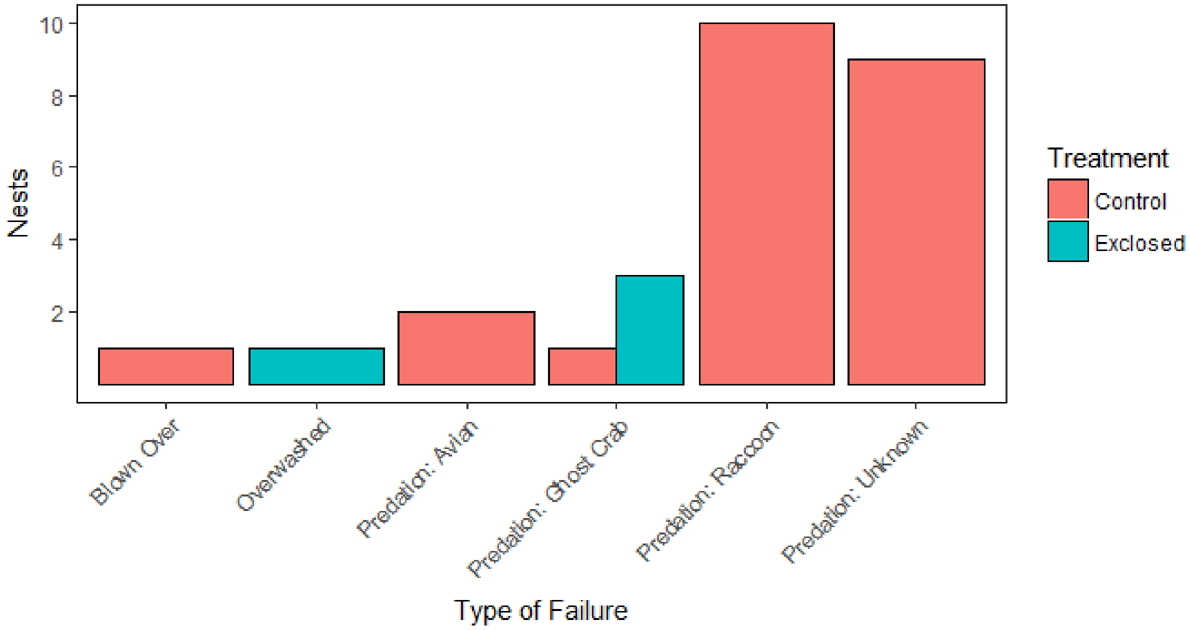

Figure 3.6: Nest Failures in 2017. The causes of nest failure among exclosed and unexclosed nests in 2017. Raccoons (*Proyon lotor*) were the top identifiable nest predator for unexclosed nests, and ghosts crabs (*Ocypode quadrata*) were the only predator of nests with exclosures.

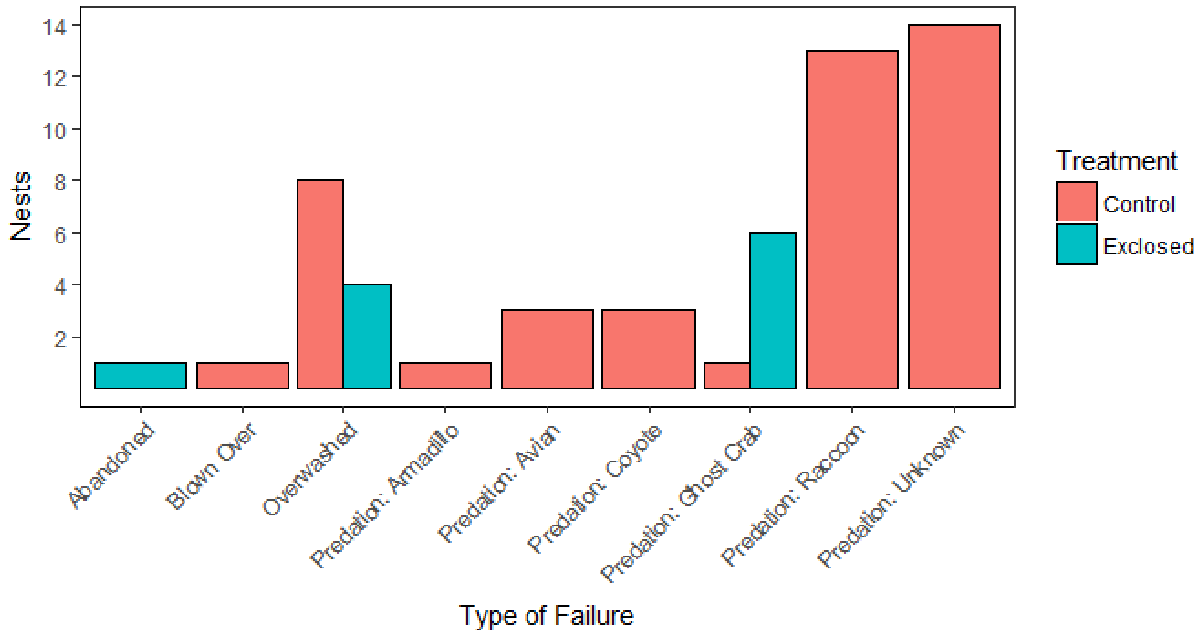

Figure 3.7: Nest Failures in 2016 and 2017. The causes of Wilson's Plover nest failure throughout both breeding seasons. The only predator to depredate nests with predator exclosures were ghost crabs (*Ocypode quadrata*), and raccoons (*Procyon lotor*) were a top nest predator for unexclosed nests.

Figure 3.8: Chick in Exclosure Photograph. A raccoon attempted to enter this predator exclosure on the same day the eggs hatched. This chick was weak, and had clearly not been brooded by the adults recently. The chick was never seen again after hatch day, and the raccoon likely indirectly caused its mortality.

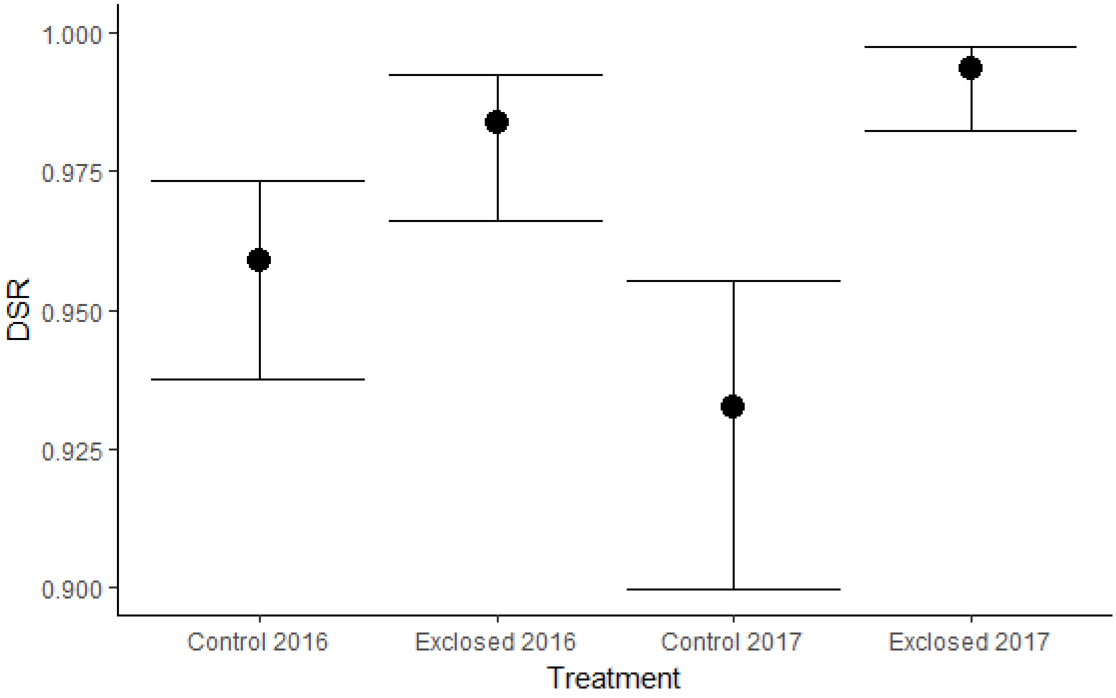

Figure 3.9: Nest Daily Survival Rate. The daily survival rate (DSR) of Wilson's Plover nests treated with and without exclosures during the 2016 and 2017 breeding seasons. In 2016, the DSR was 0.959 (CI = 0.937-0.973) and 0.984 (CI = 0.966-0.992) for control and exclosed nests respectively. In 2017, the DSR for control and exclosed nests was 0.933 (CI = 0.890-0.955) and 0.993 (CI = 0.982-0.993), respectively.

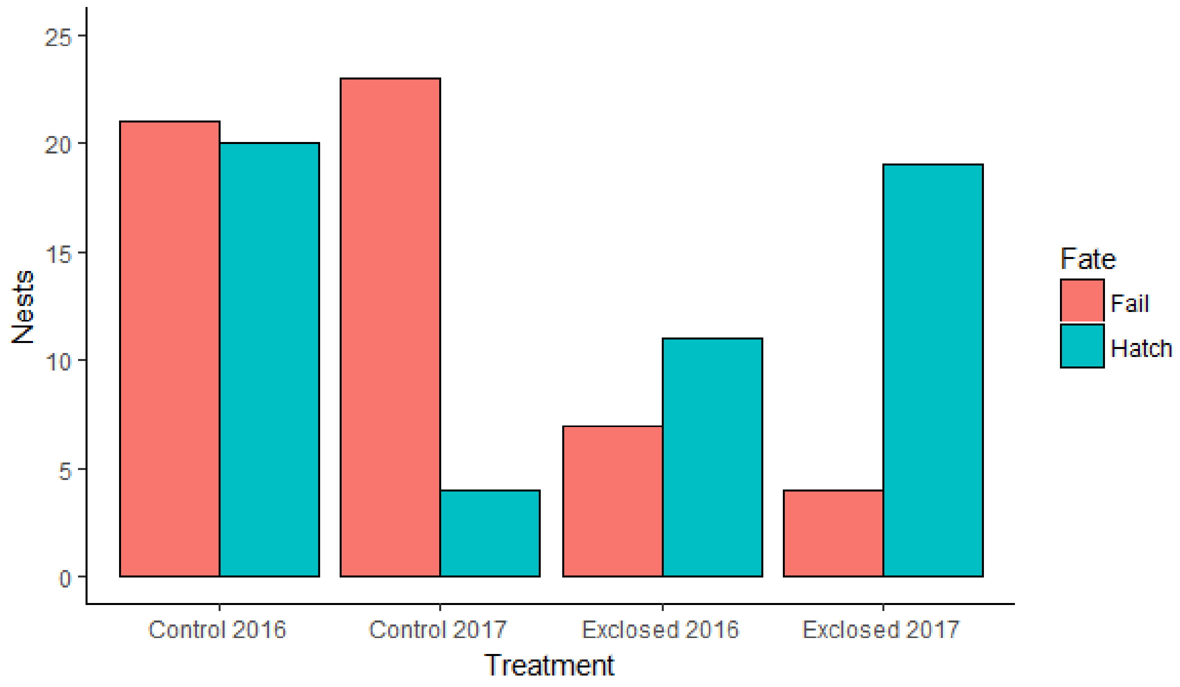

Figure 3.10: Nest Fate. The total number of nests that successfully hatched at least one egg, or failed, among each treatment in 2016 and 2017. This figure represents raw data.

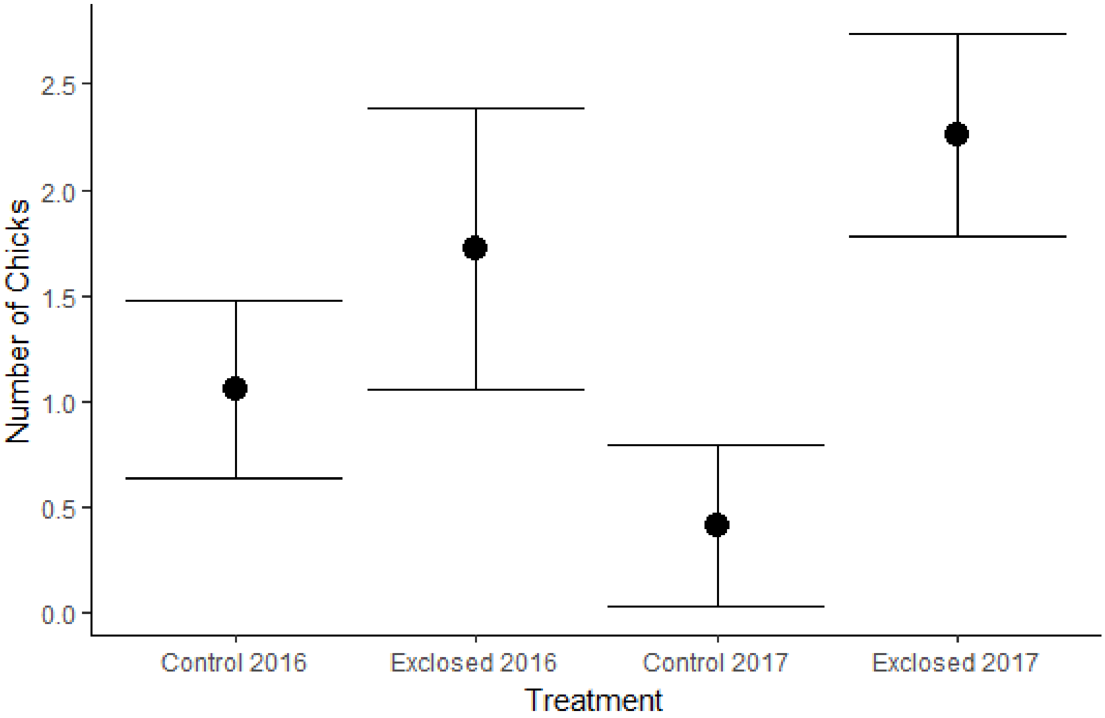

Figure 3.11: Number of Chicks Hatched/Nesting Attempt. The number of chicks hatched per nesting attempt in each treatment and year. In 2016, 1.057 (CI = 0.638-1.477) and 1.722 (CI = 1.054-2.391) chicks hatched per nesting attempt from control and exclosed nests, respectively. In 2017, 0.407 (CI = 0.026-0.788) and 2.261 (CI = 1.780-2.742) chicks hatched per nesting attempt from control and exclosed nests, respectively.

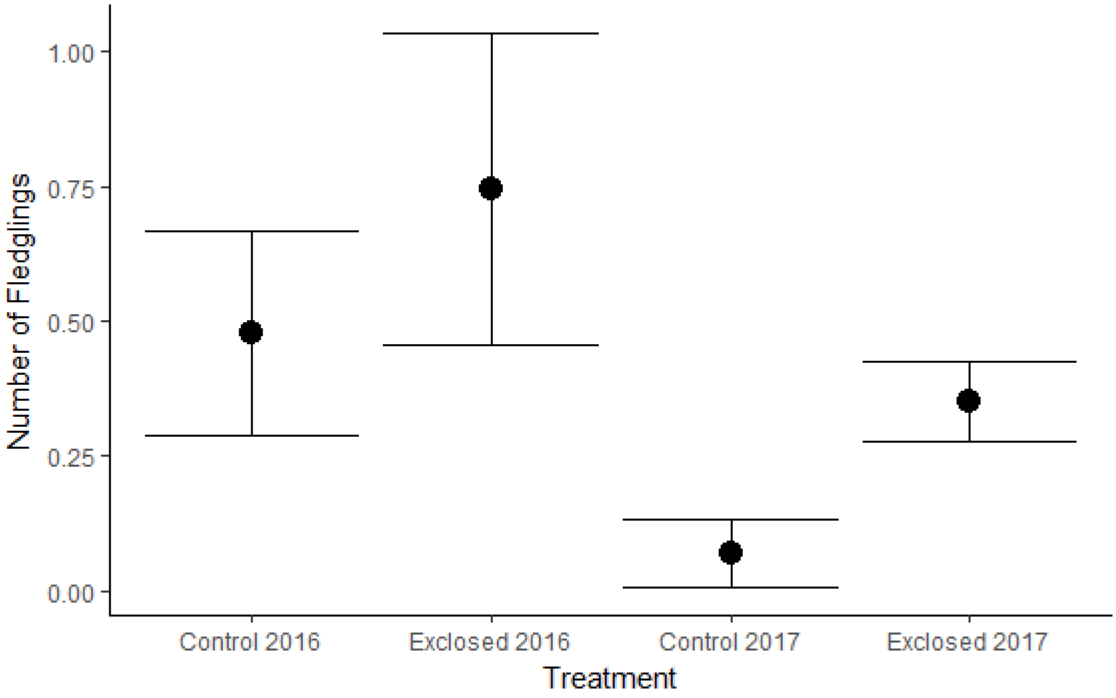

Figure 3.12: Number of Fledglings Produced/Nesting Attempt. There was no significant difference among treatments or years in the number of chicks fledged per nesting attempt on Little St. Simons Island, GA. In 2016, 0.478 (CI = 0.288-0.678) and 0.750 (CI = 0.456-1.036) fledglings were produced per nesting attempt from control and exclosed treatments, respectively. In 2017, the number of fledglings produced per nesting attempt from control and exclosed treatments were 0.068 (CI = 0.004-0.132) and 0.350 (CI = 0.275-0.424).

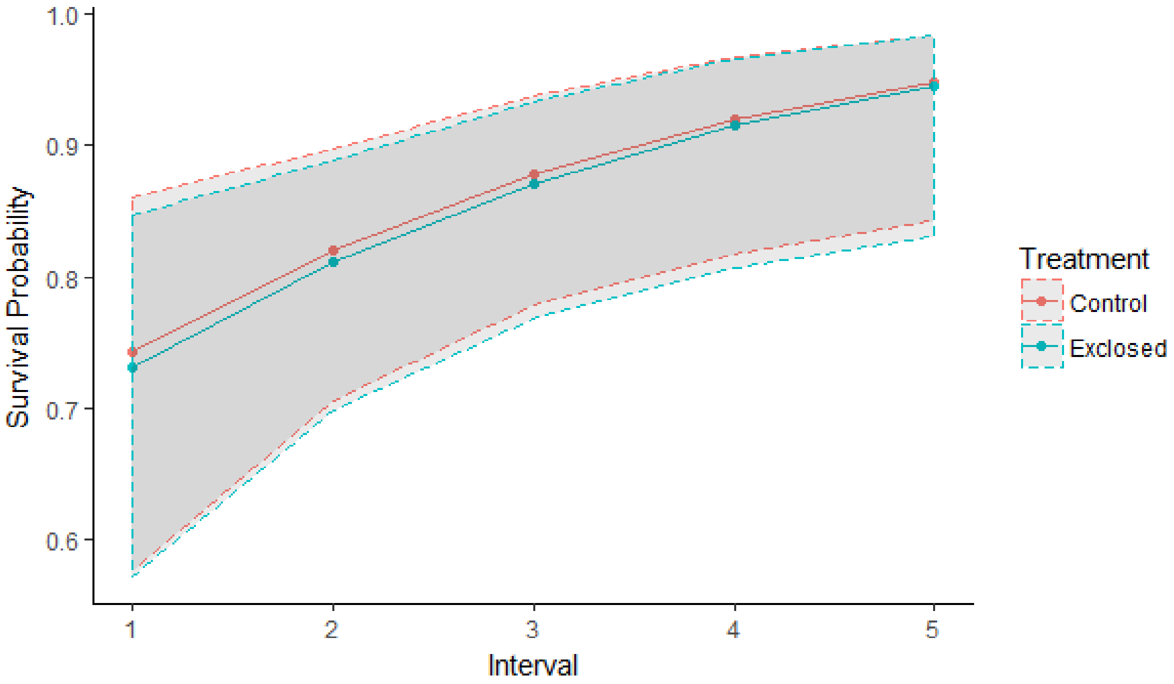

Figure 3.13: 2016 Chick Survival Probability. In 2016, the probability of survival, represented as period survival, increased through the breeding season as the chick aged.

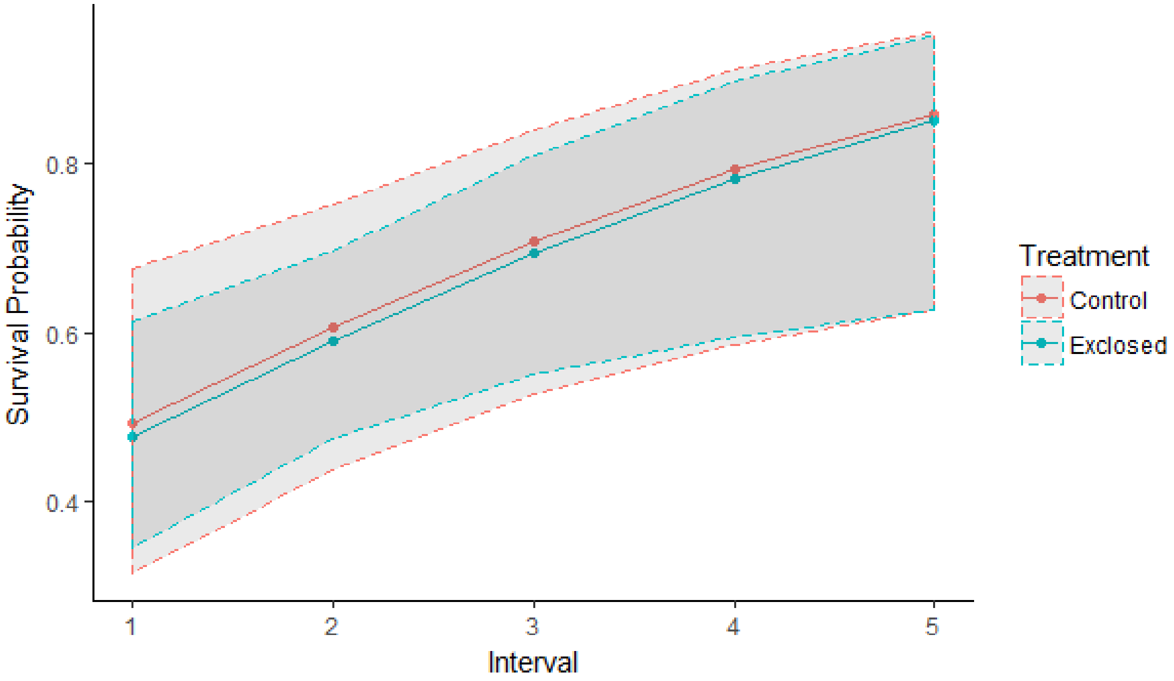

Figure 3.14: 2017 Chick Survival Probability. The probability of survival, represented as period survival, for chicks increased through the breeding season as the chick aged in 2017.

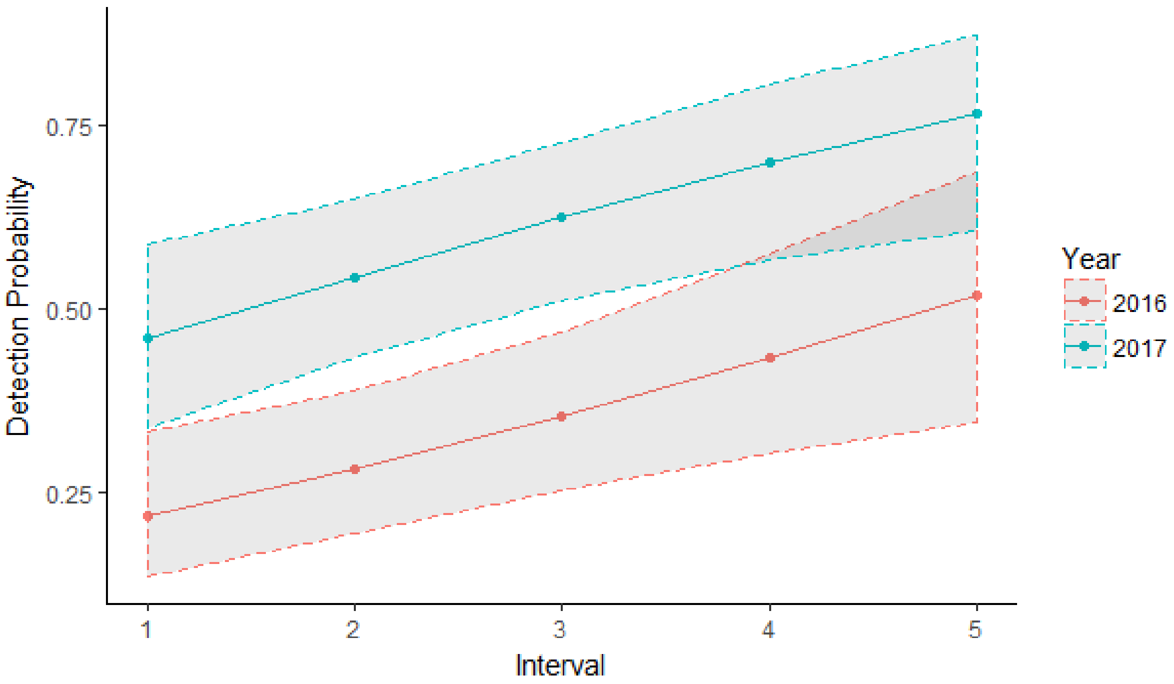

Figure 3.15: Detection Probability. The probability of detection through time for the 2016 and 2017 breeding seasons. The observers were LG and RD in 2016, and LG and KT in 2017. The detection probability was higher in 2017 than 2016.

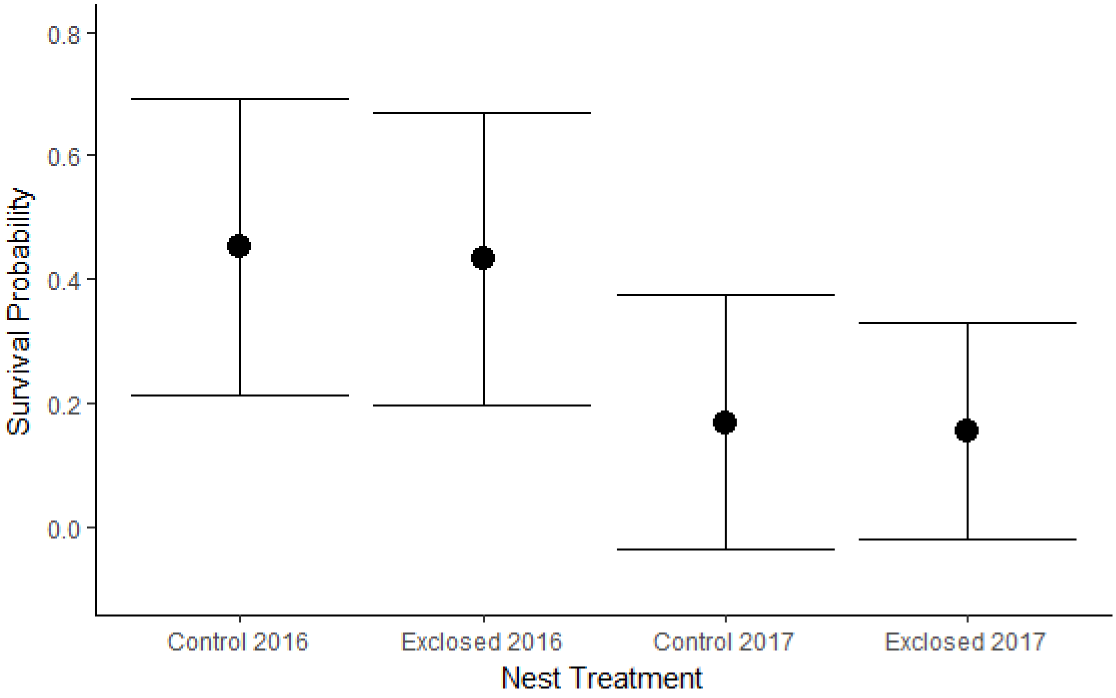

Figure 3.16: Chick Overall Survival Probability. The overall survival probability of Wilson's Plover chicks on Little St. Simons Island, GA during the 2016 and 2017 breeding seasons. In 2016, the probability of survival was 0.452 (CI = 0.212-0.692) and 0.433 (CI = 0.195-0.671) respectively for chicks hatched from control and exclosed nests. In 2017, the probability of survival was 0.168 (CI = -0.038-0.373) and 0.155 (CI = -0.021-0.330) for chicks hatched from control and exclosed nests, respectively.

CHAPTER 4

CONCLUSIONS

The results from this study demonstrate that predator exclosures are effective at increasing Wilson’s Plover nest success. The treatment effect of exclosures was the most important variable for model predictions of nest survival. High tides also played an important role in the survival of nests, especially in 2016. Tides were negatively associated with nest survival and were the second most important factor, behind treatment of exclosures, in model prediction. Since exclosures were randomly deployed in this study, multiple nests were close to, or occasionally in, the high tide wrack line. As a result, several nests within exclosures failed due to tidal overwash.

Predator exclosures successfully protected Wilson’s Plover nests from mammalian and avian predation. The only predator capable of entering exclosures and responsible for depredation of protected nests were ghost crabs. We did not visually observe direct predation by ghost crabs during this study; however, crabs were captured on trail camera images preying on eggs within exclosures. There were significantly more ghost crab burrows at nests with exclosures than unexclosed nests in this study, which causes some concern.

In this study, only one nest abandonment was documented at a predator exclosure throughout all years. In contrast, no unexclosed nests were abandoned. We believe one abandonment at an exclosed nest over two years is minimal, and no reason for concern. No adult mortality was observed either visually or through trail cameras at any exclosed nests, including the abandoned nest. Predator activity at exclosures was more frequent and disruptive in 2017 than 2016. Raccoons were observed circling and attempting to dig under exclosures in the second year of the study, and these behaviors were not seen in 2016. This delayed attraction to exclosures possibly indicates a learned behavior by predators that could result in adult mortality at exclosures in subsequent years.

More chicks hatched per nesting attempt from nests with predator exclosures since than from unexclosed nests in this study. High tides also negatively impacted the survival of chicks, likely by increasing the risk of drowning for unfledged young. Fledge rates were also higher among young hatched from exclosed nests, but this estimate did not differ significantly between treatments. Chick survival also did not significantly differ between nest treatments, and the probability of survival increased with each time interval as the chick grew and aged. This result was unsurprising since predator exclosures provide no protection for precocial chicks and are only effective at deterring predators during the incubation phase. Techniques to reduce predator disturbance throughout the breeding season will likely need to be employed to increase fledge rates, and thus, productivity.

More predator exclosures were rejected in 2017 (n=11, 32%) than 2016 (n=1, 5%) when an adult did not resume incubation within the allotted time. The exclosure design and deployment methods were consistent in both years, and exclosures were rejected consistently throughout the 2017 breeding season and across habitats. Only full clutches were exclosed to maximize the acceptance rate. Few adult birds were banded on Little St. Simons Island, so pairs were not uniquely identified. It is possible that individuals had a predator exclosure deployed at their nest in both years, and were less tolerant the second year. Mostly, though, we are unable to fully explain why so many more exclosures were rejected in the second year of the study.

This study estimated a declining growth rate among the regional Atlantic Coast population, even if predator exclosures were deployed at every Wilson's Plover nest. However, Snowy Plover demographic estimates were used for some of the parameters. More research is needed regarding Wilson's Plover demography to determine if this management technique is successful at stabilizing or increasing the population. Wilson's Plover lifespan, and juvenile and adult survival are unknown (Corbat and Bergstrom 2000), and only estimates for return rates exist (DeRose-Wilson et al. 2013). Individuals need to be uniquely banded in order to estimate demographic parameters, including number of nesting attempts per pair and departures from monogamy as well as survival. On the Atlantic Coast, a scarce number of Wilson's Plovers are uniquely banded, and a greater effort should be put forth to band individuals.

A few factors should be considered before implementing predator exclosures at a breeding site. An understanding of the diversity and abundance of the local predator community is necessary for survival of eggs, young, and incubating adults. Alternating years in which exclosures are deployed could limit habituation of predators to exclosures, and increase the acceptance rate when adults return to incubate. Exclosures are likely more effective at breeding sites during years that will experience low tides and high predation. To maximize time and resources, managers should try to predict tidal amplitude and predation rates prior to the breeding season, and target nests further away from the tide line for exclosures. Predator exclosures are only effective for the protection of eggs, and other predator management techniques will likely need to be enforced for greater chick survival and productivity.