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Predators and Anti-predator Behavior of Wilson's Plover (Charadrius Wilsonia) on Cumberland Island, Georgia

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PREDATORS AND ANTI-PREDATOR BEHAVIOR OF WILSON'S PLOVER

(*CHARADRIUS WILSONIA*) ON CUMBERLAND ISLAND, GEORGIA

by

MARY STRICKLAND

(Under the direction of C. Ray Chandler)

ABSTRACT

Predation, the major cause of nest failure in birds, is an important factor when considering management and conservation plans. The predator assemblage in an ecosystem changes each year and can cause profound differences in bird nest survival rates. Shorebirds such as Wilson's Plovers (*Charadrius wilsonia*) are ideal study species because they are declining and predator control is often a recommended component of management plans. Therefore the objectives of my research were to determine the predator assemblage of the southern end of the beach on Cumberland Island National Seashore, Georgia, and to determine how three variables affected the display rate and intensity of different anti-predator behaviors of Wilson's Plover. I quantified the predator assemblage of the beach using three methods, transect surveys, nest-site surveys, and game cameras, and compared those methods to determine the relative accuracy of each method. I also tested how the sex of the incubating adult, the age of the clutch, and the type of predator approaching the nest affected the display rate and intensity of different anti-predator responses of Wilson's Plovers. To do this I analyzed plover behavior captured by game cameras. Through this project, I was able to determine the predator assemblage on Cumberland Island, and how the relative abundance of predators affected the survival rates of Wilson's Plover nests. I determined Wilson's Plovers change their anti-predator behavior based on the sex of the incubating adult and the type of predator approaching the nest. Wilson's Plovers are declining; they rely on undeveloped beaches such as Cumberland Island as breeding sites for a sizable portion of their total population. Determining their predator assemblage provides valuable information when considering management plans for this and other species. Furthermore, understanding their anti-predator behavior shows insight as to which predators are higher risk for the adults or higher risk for the eggs.

INDEX WORDS: Relative abundance index, Nest defense, Ghost crab (*Ocypode quadrata*), Coyote (*Canis latrans*), Predation

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INTRODUCTION

Nest predation is a major cause of nest failure in birds; nearly 80 percent of all nests will fail each year (Ricklefs 1969, Cohen et al. 2009, Hardy and Colwell 2012). Nest predators can include mammals, other birds, crustaceans, reptiles, insects, and rarely amphibians. The number of species of potential nest predators varies on a latitudinal gradient, with the breeding sites closest to the equator having the largest number of possible predators (Ricklefs 1969). The abundance of nest predators in the tropics have been hypothesized to affect clutch size (Ricklefs 1969).

Predation risk varies widely among different potential predators. Carnivores such as raptors, coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) consume eggs or chicks and pose a risk to the incubating adults (Cepek 2004). Because of the decline in apex predators across the United States, there has been an increase in the presence of medium-sized omnivores (Rogers and Caro 1998). These omnivores, also called mesopredators, will typically consume the eggs in the nests or chicks, but pose a lower risk to the adults (Johnson 1970). Scavengers such as Turkey Vultures (*Cathartes aura*) will consume the eggs, but are not typically risks to the incubating adults. Yet other species (such as large mammals) can cause a nest failure not by predation, but by trampling or other forms of physical disturbance (Paine et al. 1996, Sanders and Maloney 2002).

Because of the high levels of nest failure caused by nest predators, management and conservation plans sometimes implement predator controls to increase nest survival of some bird species, particularly those with declining populations. These controls can be lethal, that is permanently removing the predator from the population by killing, or non-lethal, using barriers such as electric fencing or chemicals to induce taste aversion (Conover 1990, Mayer and Ryan

1991). For example, canids killed as a form of predator reduction in multiple studies led to the overall increase in the hatching success of some bird populations (Côté and Sutherland 1997). Predator exclosures have been used in management of Piping Plover (*Charadrius melodus,* Melvin et al. 1992) and Snowy Plover (*Charadrius nivosus*, Pearson et al. 2014) and, in both cases, nest survival increased. Studies have also tested the effects of taste aversion on predators. In some cases, the aversion technique successfully reduced nest predation by avian and mammalian predators (Conover 1990, Dimmick and Nicolaus 1990).

But is predator control routinely necessary? There are two important considerations when answering this question. First, the decision to control predators should be based on data suggesting controls are effective in the short and long term. This will not be the case if predation is compensatory (Errington 1946). Changes in the populations of one predator species could also lead to mesopredator release, which could substitute one predator for another (Goodrich and Buskirk 1995, Crooks and Soule 1999). In some ecosystems, native apex predators have decreased in numbers, with some populations needing reintroduction or supplementation with individuals from other regions (Fritts et al. 1997). In these cases, the apex predators may need to be added to the ecosystem in an effort to control the populations of the mesopredator species (Rayner et al. 2007). Ultimately, to be an effective control of predators, it must reduce an additive source of mortality and/or not give rise to new sources of additive mortality.

A second consideration is the fact that birds evolve with their predators. Natural selection favors life history traits and behaviors to cope with predation. These adaptations vary among species depending on the habitat, the size of the species, and other factors. For example, to better protect their nests, ground-nesters evolved camouflaged eggs and use ground vegetation to hide the nest (Oniki 1985, Amat et al. 2012). These adaptations do not always succeed in protecting

the nest from every predator, so birds also employ anti-predator behavior. Anti-predator behavior can be defined as any behavior used in response to the presence of a perceived threat, particularly predation threats (Curio 1975, Caro 2005). These responses are typically described as the behavior incubating adults use to protect the nest, but can also include responses of the adult to protect its own life if threatened. Species such as Sabine's Gulls (*Xema sabini*) show a variety of intensity levels for their anti-predator responses ranging from distraction techniques to lure the predator away from the nest to physical attacks on the predator (Stenhouse et al. 2005).

The risk posed by predators, and the potential value of control, is especially important in areas where humans have impacted the habitat (Vitousek et al. 1997). A decrease in habitat quality means that the relative importance of predation as a source of mortality may increase. For example, edge-effects caused by the fragmentation of ecosystems may increase exposure to nest predators and increase rates of nest predation (Andrén 1992, Crooks and Soulé 1999). These compounding effects can lead to population impacts such as the declines seen in forest-living corvids as their native habitats were converted to agriculture (Andrén 1992). For birds, habitat loss is the source of extinction risk for nearly 70 percent of the species listed as threatened (over 1,000 species); the next highest source of extinction risk was introduced predators and human persecution (Owens and Bennett 2000).

Not only are humans degrading habitats, but as humans move into natural ecosystems they introduce or facilitate novel predators (Prange et al. 2003). Novel predators are species introduced into an ecosystem that prey species have no experience with. Adding novel predators into an ecosystem can result in levels of predation from which prey populations may not fully recover (Skutch 1967, Ricklefs 1969, Dowding and Murphy 2001). This could be because prey species have no evolutionary experience with the novel predators (Sih et al. 2010), or that novel

predators may reach high densities without another predator species to control their population growth. If a prey population can acclimatize or adapt to the presence of a novel predator, there could still be negative effects on the food web in that ecosystem, leading to problems in the native predator populations (Strauss et al. 2006).

Shorebirds are a good example of the key role predation may play in declining populations. Many species of shorebirds have been declining over the past few decades due to anthropogenic disturbances to breeding habitats and increased populations of both native and introduced predators (Corbat 1990, Brown and Brindock 2011). The predators encountered by shorebird species such as Piping Plover, Snowy Plover, and American Oystercatcher (*Haematopus palliatus*) could be prime targets for predator control (Sabine 2005, Cohen et al. 2009, Hardy and Colwell 2012).

Most shorebirds are ground-nesters in open and exposed habitat among dune systems, which is thought to allow for faster predator detection (Amat and Masero 2004). Although this allows the adults to escape much faster, this leaves the nest and eggs more vulnerable (Downs and Ward 1997). Thus, shorebirds have camouflaged eggs and use some vegetation and substrate to cover and camouflage their nests along with the use of anti-predator behavior. Without effective behaviors to discourage predators, nest predation might be even higher than the fairly high rate they currently show (Ricklefs 1969). Incubating adults need the ability to distinguish what level of risk warrants each anti-predator tactic (Curio 1975). This assessment may be difficult in the case of novel predators (Strauss et al. 2006).

Wilson's Plovers (*Charadrius wilsonia*) are an ideal species to address these issues. Like many shorebirds, they nest on open, exposed ground within beach habitat, and they are under threat from human development (Tomkins 1944, Bergstrom 1982). Predators, including novel

predator species and mesopredators, seem to be the primary source of nest failure (Corbat 1990, Sabine 2005), and there are suggestions from other studies that predator control may be needed to protect this species (Cox 2015).

Little is known about how these plovers deploy anti-predator behavior in response to approaching predators (Bergstrom 1988b). The use of anti-predator behavior against predators approaching the nest presumably allows Wilson's Plovers to protect their nests in some instances against certain predators. Variations in anti-predator responses among other species of shorebirds suggest that key variables include the age of the clutch being incubated, the sex of the incubating adult, and the species or type of predator approaching the nest (Brunton 1990). To understand the role of the predators of Wilson's Plovers and make intelligent decisions about control, we need information on three areas: the predator community, the risks specific predators pose to nest survival, and how plovers respond to those predators.

First, the composition of the predator community affects the type of predators Wilson's Plovers will encounter at their nests. Wilson's Plovers face a variety of predators within their breeding habitat. Presumably this assemblage will include species that are primarily a risk to adult birds or larger chicks (e.g., Accipiters), those that threaten both adults and eggs (e.g., coyote), and those that are primarily a threat to eggs and small chicks (e.g., ghost crabs [*Ocypode quadrata*], trampling by horses). Although nest predators of Wilson's Plovers have been described (e.g., Sabine 2005, Cox 2015), there has been no attempt to describe the entire assemblage of nest predators and threats in the dune habitat used by these plovers.

Second, the risks each predator species pose to Wilson's Plover nest survival affect the type or amount of controls that might be implemented. Large mammals such feral horses (*Equus caballus*) and white-tailed deer (*Odocoileus virginianus*) may not threaten shorebird nests on a

regular basis, but can cause nest failures both by consuming the eggs or by trampling the nest (Sabine et al. 2006, Cox 2015). These species' daily activities in the dune system can also have negative impacts on the reproductive success of Wilson's Plovers and other shorebirds by initiating nest defense and attracting attention (Cox 2015). Feral pigs (*Sus scrofa*) are infrequent nest threats, but will eat eggs and alter the habit (Cox 2015). Apex predators such as coyotes and bobcats can be major causes of nest failures, but they also pose risk to the incubating adults. In particular, coyotes are an introduced novel predator in the southeast United States that thrive in human disturbed habitats (Hill et al. 1987). Evidence of coyote presence on Georgia's barrier islands has occurred recently, with studies as recent as 2005 showing no evidence of coyote presence on barrier islands (Corbat 1990, Sabine 2005). Finally, an array of avian and mammalian mesopredators pose high risk to eggs and chicks, but little to adults. Avian predators such as crows (*Corvus ossifragus* and *C. brachyrhynchos*) and Laughing Gulls (*Larus atricilla*) pose risks during the day on plover nests and chicks, and pose only small risks to the adults (Corbat 1990, Santisteban et al. 2002). Mammalian mesopredators such as raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and nine-banded armadillos (*Dasypus novemcinctus*) were the most frequent nest predators in previous studies (Corbat 1990, Sabine 2005).

The risk posted by some species is not agreed upon. A good example is the ghost crab, which is abundance on coastal beaches. Ghost crabs may or may not be major threats of shorebird nest success (Watts and Bradshaw 1995, Staus and Mayer 1999, Wolcott and Wolcott 1999). Along the northeastern Atlantic coast, researchers found that few Piping Plover nests were directly depredated by ghost crabs (Wolcott and Wolcott 1999), whereas other studies

found higher levels of depredation by ghost crabs (Loegering et al. 1995, Watts and Bradshaw 1995, Staus and Mayer 1999).

Third, we need to understand how Wilson's Plovers respond to nest predators and threats. One variable that could affect how Wilson's Plovers react to an approaching predator is the age of the clutch being incubated (Sordahl 1986). Anti-predator response intensity might increase in incubating adults as the value of the nest changes (Kazama et al. 2011). If the clutch is close to its expected hatching date, we might expect the intensity of the anti-predator behavior to be higher than earlier responses to the same type of predator, suggesting that adults might be willing to take greater risks in defending the nest (Sordahl 1986, Brunton 1990). If Wilson's Plovers increase their anti-predator behavior intensities as the clutch ages it would suggest that the plovers perceive a greater cost to losing a clutch near the hatching date than losing a recently laid clutch (Brunton 1990). Brunton (1990) found significant increases in the intensity of anti-predator behavior as clutches aged in Killdeer (*Charadrius vociferous*). Cairns (1982) concluded that Piping Plovers displayed more frequently with broken-wing display as the clutch reached its hatching date. However, this could have been caused by the incubating adults becoming sensitized to the multiple approaches made by the researchers (Knight and Temple 1986). In another study, St. Clair et al. (2010a) found that the Two-banded Plover (*Charadrius falklandicus*) did not react differently to predators based on the age of the clutch, but the adults changed their reactions based on the size of the clutch.

A second variable that could affect how Wilson's Plovers react to an approaching predator is the sex of the incubating adult. Wilson's Plovers have a sex-specific incubation pattern that could affect the anti-predator behavior displayed (Bergstrom 1986, Cox 2015). Males incubate at night, whereas the females incubate during the day (Bergstrom 1986). Behavior could

change between night and day because risk to the incubating adults is increased at night due to reduced visibility (Amat and Masero 2004). Sexes may evaluate risk differently as well. Other research has studied the differences in the reactions between sexes in species such as the Black-tailed Gull (*Larus crassirostris*, Kazama et al. 2011), Barred Warbler (*Sylvia nisoria*, Polak 2013), and Red-backed Shrike (*Lanius collurio*, Tryjanowski and Golawski 2004). Some of these studies suggest that males show higher intensity responses than females (Kazama, et al. 2011). However, Tomkins (1944) hypothesized that female Wilson's Plovers responded more frequently with broken-wing displays to distract predators and lure them from her nest than males, suggesting that female Wilson's Plovers show higher intensities of anti-predator behavior than males.

The final variable that could change the anti-predator responses displayed is the type or species of predator approaching the nest. The type of predator approaching the nest could elicit different responses from incubating plovers depending on the risk that predator poses to the adult and its eggs (Brunton 1990, Walters 1990). Presumably adult plovers will evaluate the risk the threat poses to themselves and their eggs or chicks, as well as the probability that defense would be successful. A smaller predator that is a high risk to the nest but low risk to the adult might elicit intense attacks. A large predator that is dangerous to adults might elicit more circumspect distraction displays. All of these assumptions are based on the idea that plovers can discriminate different threats from predators and determine risk. Studies on Black-tailed Gulls (Kazama et al. 2011), Cardinals (*Cardinalis cardinalis*, Gottfried et al. 1979) and American Robins (*Turdus migratorius*, Gottfried et al. 1979) have shown variations in responses based on different types of predators. Others, such as Two-banded Plovers (St. Clair et al. 2010a) and Sabine's Gulls (Stenhouse et al. 2005) have not shown variations in responses based on the type of predator.

The objective of this study is to quantify the predators and anti-predator behavior of Wilson's Plovers on Cumberland Island, Georgia. I addressed three specific questions. First, what is the assemblage of predators that may threaten breeding Wilson's Plovers? Although many studies quantify predators at bird nests, few try to estimate the relative abundance of the overall predator community. I used three different methods, transect surveys, nest-site surveys, and game cameras, to determine the relative abundance of the different predators that may threaten plover nests. Second, which predators or threats pose the greatest risk of nest loss? Even though predators are present, not all may be constant nest threats. I located and monitored Wilson's Plover nests, and determined causes of failure by evidence at the nests.

Third, how do different variables affect the intensity and anti-predator behavior of Wilson's Plovers? I used photos captured by game cameras to analyze how the anti-predator behavior of Wilson's Plovers were affected by the sex of the adult, the age of the eggs, and the type of predator or threat approaching the nest.

METHODS

Study Site

This study was conducted from March-August, 2014 and 2015, on Cumberland Island National Seashore (CINS), a minimally developed barrier island with limited public access. It is the southern-most barrier island on the Georgia coast. A majority of the island is owned by the National Park Service, while small parts of the island are privately owned. The 29 km of undeveloped beach are a breeding site for shorebirds such as Wilson's Plovers, American Oystercatchers, Least Terns (*Sternula antillarum*), and Willets (*Tringa semipalmata*) (Sabine et al. 2006). The dune system on CINS varies in width from 30 – 300 m along the entire length of the island (Sabine 2005, Cox 2015). However, a majority of the shorebirds nest in the southern-most 7 km and northern-most 7 km of CINS (Sabine 2005, Cox 2015). CINS is home to a diverse assemblage of potential shorebird predators and nest predators such as coyotes, raccoons, crows, Virginia opossums, feral pigs, ghost crabs, and many other species. CINS is also home to a population of approximately 150 feral horses that roam the entire island.

My study site included approximately 7 km of beach along the southern end of the island (Figure 1). I divided the study site into four different areas ranging from 1.5 – 1.9 km in length depending on the relative amount of human activity in the areas and the density of Wilson's Plover breeding pairs in those areas (Figure 2). Within this study site, the dune system ranged from 30 – 170 m wide, and Wilson's Plovers used a large portion as possible nesting habitat (Cox 2015, personal observation). Approximately 30 – 50 pairs of Wilson's Plovers nest within the study site each year (Cox 2015, personal observation).

Population Survey

I surveyed the length of the study site throughout the peak of the breeding season (May and June) of 2015 to map the distribution of Wilson's Plover breeding pairs. Wilson's Plovers are territorial and maintain well-defined boundaries during the breeding season. Observations were conducted from a National Park Service vehicle between 7 and 10 am for approximately 5.7 km. The final 1.3 km of beach were surveyed by foot. Each breeding pair seen was recorded in each area of the study site.

Nest Success

To locate Wilson's Plover nests, I repeated followed a line transect parallel to the beach (Bergstrom 1988a). Once the tracks of adult plovers were located, I followed the tracks until a nest was located (Brown and Brindock 2011, Cox 2015). This was an efficient way of locating nests because plovers walk to nests more often than they fly to the nest (Bergstrom 1988a). Once a nest was located, I recorded a global positioning system (GPS) point and described the nest location within the dune system.

Once found, I counted the eggs in the nest and then floated them to determine the approximate date the clutch was initiated (Liebezeit et al. 2007, St. Clair et al. 2010a). I used clutch initiation date to predict the nest hatching date. Each nest was checked every 4 – 9 days so that nest fate could be determined as accurately as possible without attracting too much attention to the nest from repeated visits (Brown and Brindock 2011, Hardy and Colwell 2012). The distance I approached the nest to check depended on the location of the nest. Some nests could be checked from a distance of 5 m, others had to be approached to within 1 m. Daily checks were made once the chicks were heard peeping or the eggs were pipped, typically within two days of their hatching date (Hardy and Colwell 2012).

If nests failed, I analyzed the evidence around the nest site to determine the cause of the failure. Evidence could consist of the damage caused to an eggshell that was left behind, the predator tracks within 1 m of the destroyed scrape, or if the tide clearly washed over the area where the nest had been previously. In some cases, the cause of failure could be attributed to a predator, but not any particular species. For these nests, their cause of failure was predation, but the predator was listed as unknown.

The Mayfield Nest Survival analysis in Program MARK was used to determine the daily nest survival rates in 2014 and 2015. I used chi-square analyses to determine the differences in the amount of nest failures attributed to each predator or threat species between 2014 and 2015. I also used chi-square analyses to determine the relative importance of each predator or threat species in the survival rates of Wilson's Plover nests.

Relative Abundance of Predators

I estimated the predator community within the study site using three methods. Each gave an estimate of the relative abundance of potential predators in the habitat used by nesting Wilson's Plovers. Wilson's Plover nests can be destroyed by predators (who benefit from the interaction by eating plover eggs or chicks) or by species that damage or destroy the nest incidentally (e.g., horses that trample eggs but don't eat them). I will often refer to all of these nest threats as "predators" although all species do not meet the ecological definition of a predator.

First, I used transects placed throughout the study site to estimate the relative abundance of potential predators based on the frequency of tracks left in the sand. In the sandy habitat used by Wilson's Plovers, predators routinely leave tracks that can be readily identified (Figure 3). Transect surveys were designed to estimate the predator community that might threaten plovers

or their nests. I used stratified random sampling to place 32 transects within the study site that extended from the edge of the plover breeding habitat (scrub on the landward side) to the high-tide line, each perpendicular to the shoreline (Figure 4). These transects were surveyed three times during the 2015 season. The first survey was completed April 3 – 4, 2015, during plover territory establishment and nest preparation. The second survey was completed May 12 – 14, 2015, prior to the peak of nesting. The final survey was completed June 19 – 21, 2015, after the peak of the breeding season.

On each transect, I counted the number of times a set of tracks of any predator or threat crossed the line (Pulliainen 1981). I was able to identify tracks for the following species: coyotes, bobcats, feral horses, white-tailed deer, feral pigs, raccoons, crows, and nine-banded armadillos (Figure 3). Tracks found were assumed to be recent (within 24 hours) because wind, rain, and shifting sand obliterated tracks quickly. Thus, my transects sampled predator activity over a short snapshot of time. If a crow flew over the transect during the survey, it was also included. In the cases when a single individual crossed a single transect multiple times, only one crossing was tallied (Pulliainen 1981). The predator abundance estimates were standardized to the number of crossings per 100 m of transect.

I also estimated the relative abundance of ghost crabs by counting ghost crab burrows within 5 m of the same transect lines. The burrow activity (active vs. inactive) and burrow width, which is correlated with the size of the carapace of the ghost crab, were estimated for each burrow (Turra et al. 2005). An active burrow was defined as a burrow with tracks leading directly into the burrow, whereas an inactive burrow was any burrow with no tracks (Hobbs et al. 2008). Lizard burrows, though similar in size, but not in shape, were not included in the census.

If lizard tracks, most likely six-lined racerunner (*Aspidoscelis sexlineata*), were seen entering a ghost crab-shaped burrow, that burrow was not counted.

Wolcott and Wolcott (1999) used ghost crabs with carapace widths of approximately 43 mm as predators in their experimental study due to the assumption that ghost crabs need to be a certain size to manipulate shorebird eggs. However, their data suggested that ghost crabs only attack eggs that are already cracked or rotting and, thus, easier to manipulate and crack (Wolcott and Wolcott 1999). The number of burrows within each transect was standardized to the number of burrows per 100 m.

The second approach I used to quantify the relative abundance of predators was to estimate the proportion of nest sites with each species present. To do this, I quantified tracks or sign of potential predators within the vicinity of Wilson's Plover nests (defined as within 10 m of a nest site). The presence and absence of predators found within a plover nest site was determined by the evidence left by predators during each nest check which included tracks, rooting, burrows, or fresh scat. Tracks could be identified for the following species: feral horses, white-tailed deer, coyotes, feral pigs, bobcat, Virginia opossum, raccoon, crows, nine-banded armadillos, and human tracks other than my own. Other species that were noted but not considered threats to the nest included Willets, Mourning Doves (*Zenaida macroura*), Wild Turkey (*Meleagris gallopavo*), Least Terns, gopher tortoises (*Gopherus polyphemus*), and diamondback terrapins (*Malaclemys terrapin*).

I also counted ghost crab burrows within 10 m of the nest when the nest was first located regardless of stage of incubation at that time. The burrow count was then repeated once the fate of the nest, either success or failure, was determined. The number of burrows around each nest site was standardized to the number of burrows per 1 m^2. To compare the number of burrows

around nest sites to those found within transects, I standardized the number of burrows within the transects to burrows per 1 m^2.

Finally, actual encounters with potential predators or threats were captured on game cameras placed at randomly selected nests. An encounter was tallied each time a predator was present in the field of view (St. Clair et al. 2010b). The encounters were recorded using Reconyx PC900 and PC800 Hyperfire cameras secured onto stakes approximately 1 – 3 m from the nest (Sabine et al. 2005, Cox 2015). The close proximity increased the cameras' accuracy with which the total number of predation events at each nest was estimated. Multiple studies have shown that the close proximity to the nest has no effect on nest survival (Brown et al. 1998, Pietz and Granfors 2000, Sanders and Maloney 2002, Renfrew and Ribic 2003). I set the cameras on motion-sensing photo capture during the day and infrared-sensing photo capture at night (RECONYX 2012). Once the camera was triggered, it would continue to photograph the movement, up to two frames per second, until no more movement was sensed (RECONYX 2012). The rate of photo capture did not change between day and night settings (RECONYX 2012).

Game cameras captured encounters involving potential predators or threats such as coyotes, feral horses, white-tailed deer, nine-banded armadillos, humans (other than myself or my assistants), ghost crabs, crows, feral pigs, Virginia opossums, and Turkey Vultures. Other species seen on the game cameras that were not considered a risk to the nest or the incubating adult included Willets, Mourning Doves, Wild Turkeys, and Savannah Sparrows (*Passerculus sandwichensis*). An encounter was considered complete when the game camera no longer captured consecutive photos with the same individual. For each event, I recorded the survival or loss of the nest and the survival or death of the incubating adults.

Plover Response to Predators

I interpreted the anti-predator behavior of the incubating plovers from the game camera photos when the type of response could be determined. The response of the plover to the other species in the photos was placed into one of three categories: no response, fleeing, or nest defense. I recorded no response when the plover showed little to no change in behavior and continued its incubation of the nest, and further described the behavior as either no change in incubation behavior or crouching closer to the nest. Fleeing was recorded when the plover disappeared from the field of view and did not return to the nest, and I noted whether the birds ran from the nest on foot or flew away. Nest defense was recorded when the plover showed some form of defensive behavior. In the nest defense category, I identified six behaviors, flushing from the nest, broken-wing display, flying after the predator, charging at the predator on foot, a spread-wing display, and swooping or diving at the predator. The stage of incubation was determined for each predator encounter with the use of the date and time stamp on the photos.

Analysis

Transects, nest searches, and game cameras provide three different estimates of the predator community impacting Wilson's Plover. Thus, a comparison of techniques is of interest. To do this, I used a paired test to compare the relative abundance estimates of each potential predator from the three methods. I then ranked the estimates and used a Spearman's rank correlation to compare the methods' relative abundance estimates of potential predator species to the other potential predator species.

The frequency of each species present on transects was compared to every other predator species to determine the most common predators within the study site. These frequencies were compared to the frequency of predators found in the nest-site surveys. The comparison of these

two surveys would highlight predator species that do not randomly encounter plover nests, but rather those predator species that actively search for plover nests. If the game cameras affected the presence of a particular predator, I would expect to see a significant difference between the number of predator encounters at nests with the game cameras and the number of predators present at all of the plover nests.

I used the nest-site surveys and nest survival rates from the game cameras to determine the relative risk of each predator species to plover nest survival. This quantified risk as a function of the predators found in the nest sites multiplied by the odds of those predators causing a nest failure.

I then used a bivariate fit regression to compare the number of days captured by game cameras at each nest to the number of predation events captured. I used contingency tables and chi-square analyses to test if the species of predator that came within the field of view of the game cameras affected the outcome of the nest.

Contingency tables and likelihood ratio chi-square analyses were used to test the anti-predator behavior shown in relation to the sex of the incubating adult, the nest fate, the predator approaching the nest, the proximity of particular predators to the nests, and the time of day.

RESULTS

Population Survey

Approximately 42 breeding pairs of Wilson's Plovers were sighted within the study site during the peak of the breeding season (between May and June 2015). Within the study site, the mean number of breeding pairs was 6.07 ± 1.16 SE pairs per km (range 3 – 12 pairs).

Nest Success

I located a total of 136 nests during the summers of 2014 and 2015, 63 in 2014 and 73 in 2015 (Figure 5). Of these, 39 hatched at least one egg (29%) and 95 failed (70%) (Figure 6). For two nests (1%), the outcomes could not be determined, so those were removed from the nest survival analyses. Failures in 2014 and 2015 were due to depredation or trampling (84%), washing out (3%), abandonment by the adults (5%), or failure for an unknown reason (5%) (Figure 7). Nests were significantly more successful in 2014 (37%) than in 2015 (16%) (Mayfield nest survival estimates, $p < 0.01$).

Of the 80 nest failures attributed to predators, I was able to determine the predator for 42 (52%) of the nests (Table 1, Figure 8). Six species depredated 23 of the 61 nests in 2014 (38%) and three species depredated 57 of the 73 nests in 2015 (78%). In both years, predation was unequal across predators, with coyotes and crows accounting for a majority of the nest failures. In a few cases, ghost crabs were a secondary predator that would eat eggs left in the nest after another predator ate an egg. The proportion of nests lost to each predator were similar between 2014 and 2015, except for increases in depredations by coyotes, crows, and unknown predators ($X^2 = 12.75$, df $= 4$, $p = 0.01$, Table 1).

Relative Abundance of Predators

Based on the transect surveys, Wilson's Plovers are exposed to a diverse assemblage of potential predators (Figure 9). First, I determined predator abundance among the transects for all of the different predator species. There were three predator species present in over 50% of the transects (Table 2). Ghost crabs, found on 100% of the transects, had an average frequency of 30.06 ± 2.14 SE ghost crab burrows per 100 m of transect. There was variation in the abundance of ghost crab burrows among the four sections of the study site, with the mean frequency ranging from 2.4 – 4.4 burrows per 100 m (Kruskal-Wallis, $X^2 = 31.81$, df $= 3$, p <0.01). Coyotes and feral horses were found on a majority of the transects. The next three most common predator species found crossing the transects were nine-banded armadillos, white-tailed deer, and feral pigs. The crow and the raccoon were each present on one transect, and neither the bobcat or the Virginia opossum were detected on any of the transects.

I found that the nest-site surveys estimated a predator community similar to that of the transect surveys, with the most common predators being ghost crabs, feral horses, and coyotes (Table 3). The next three most common species were white-tailed deer, crows, and nine-banded armadillo. The mean number of ghost crab burrows found in nest-site surveys was 0.037 ± 0.004 SE burrows per m^2. There was significant variation in the density of ghost crab burrows among the four areas of the study site, with means ranging from 0.024 – 0.073 burrows per m^2 (Kruskal-Wallis, $X^2 = 8.63$, df $=3$, p $= 0.03$). Because nests could be located during any of the three incubation stages, I tested whether the age of the clutch affected the number of burrows present around the nest. Regardless of the estimated age of the clutch in question, there was no significant change in the number of burrows present at the nest sites (Kruskal-Wallis, $X^2 = 14.85$, df $= 15$, p $= 0.46$) (Figure 10, nest sites).

The game cameras detected similar predators as the other techniques. Of the species captured by the game cameras, feral horses, coyotes, and ghost crabs made up the largest proportion of the actual predation events at 45 different nests (Table 4). Of those nests, 41 had one or more predator-encounter events. Among the 45 nests, I captured approximately 555 camera days with an average of 12.3 camera days per nest. Across those 45 nests, a total of 177 predator-encounter events occurred, averaging approximately 0.25 events per day (Figure 11, df $=1, 44, F = 18.40, p <0.01$). The presence of a game camera at a nest did not affect the outcome of the nest ($X^2 = 1.69$, df $=1$, $p = 0.43$). However, I removed the game cameras before the end of the 2015 breeding season due to evidence of learning by crows. Despite the learning demonstrated at the end of the breeding season in 2015, the nests without game cameras were just as likely to fail to crows as those with game cameras ($X^2 = 2.01$, df $= 1$, $p = 0.16$).

The type of predator approaching the nest significantly influenced the nest survival of those 45 nests (Figure 12, $X^2 = 51.91$, df $= 5$, $p <0.01$). Coyotes in the field of view depredated nests in 13 of the 26 coyote events (50%), crows depredated nests nine out of the 17 events (53%), and every other threat caused nest failures in less than 20 percent of their events. Nest survival was not affected by the incubating adult being the male (16 of 77 events, 21%) or the female (11 of 86 events, 13%) ($X^2 = 2.04$, df $= 1$, $p = 0.15$), nor was it affected by the age of the clutch (Table 6, $X^2 = 7.81$, df $= 3$, $p = 0.05$).

Comparison of Techniques

All three methods used to estimate the predator assemblage gave similar results. Transects estimated predator frequency similar to that of the nest-site surveys (Paired-t $= 0.23$, df $= 9$, $p = 0.82$, Table 5), and both methods ranked predator abundance similarly ($r_s = 0.89$, p <0.01). Predator frequency estimates differed between nest-site surveys and the game cameras

(Paired-t = 2.30, p <0.05). However, the two methods still estimated similar rank abundance (r_s = 0.86, p < 0.01, Table 5). Thus, nest-site indices were associated with higher detection by cameras, but at a slope less than 1.0 (Figure 13). Finally, the transects and the game cameras showed similar predator frequencies (Paired-t = 1.42, p = 0.19) and similar rank orders (r_s = 0.76, p = 0.01, Table 5).

Transects and nest-site surveys gave similar estimates of ghost crab abundance. I found an average of 0.034 ± 0.003 SE burrows per m^2 in the transects which was not significantly different from the burrows found in the nest sites (X^2 = 1.34, df = 1, p = 0.25). However, during the establishment period of the breeding season, the first five weeks of the breeding season, the nest sites showed an average of 0.05 ± 0.008 SE burrows per m^2 in the nest sites whereas the transects showed 0.03 ± 0.003 SE burrows per m^2 (Figure 10, df =1, 2, p = 0.04).

Plover Response to Predators

To determine if the age of the clutch affected anti-predator behavior, I divided the incubation period into three categories: early, mid, and late. The age of the clutch was considered early if the clutch was still being laid to 9 days old, mid if the clutch had been incubated for 10 – 18 days, and late if the clutch had been incubated for 19 – 27 days. I found that the age of the clutch did not influence the reaction shown by the incubating adult, (Figure 14, X^2 = 8.27, df = 4, p = 0.22).

The sex of the incubating adult did affect the type of reaction shown (Figure 15, X^2 = 29.09, df = 2, p <0.01), with males displaying fleeing behavior most frequently (39 of 78 events, 50%) and females most frequently displaying defense behavior (47 of 89, 52%). However, the incubation pattern of the plovers may have biased these data, because there was a significant difference in the frequency of the anti-predator behavior displayed between nighttime (when

primarily males incubate) and daytime (primarily when females incubate) (Figure 16, $X^2 =$ 35.84, df = 2, p <0.01). Fleeing behaviors were displayed mostly at night (40 of the 74 events, 54%), whereas defense behaviors were displayed mostly during the day (54 of the 93 events, 58%).

The differences between the anti-predator behaviors displayed during the day compared to those displayed at night could have also been attributed to the type of predator approaching the nest, which differed between night and day (Figure 17, $X^2 = 72.69$, df = 5, p <0.01). Coyotes were mainly encountered at night, whereas crows were encountered during the day. Trample threat events, which include events with feral horses and white-tailed deer, and ghost crab events occurred during the day and at night. Finally, the no threat group, including species such as Willets, Mourning Doves, Wild Turkeys, and Savannah Sparrows were encountered during the day.

The differences in the species events between day and night led to the two sexes encountering a different assemblage of predators (Figure 18, $X^2 = 44.82$, df = 5, p <0.01). Most notably, encounters with coyotes (26 of the 27 total coyote occurrences, 96%) were almost exclusively by male plovers.

The type of predator or threat from the predator approaching the nest influenced the type of anti-predator behavior displayed by the incubating adult (Figure 19, $X^2 = 175.56$, df = 10, p <0.01). Coyotes caused plovers to flee in all coyote-encounter events, and crows and ghost crabs elicited defense anti-predator behavior from the incubating adults. Trample threats within 3 m of the nest elicited mostly defense behavior, whereas if trample threats were farther than 3 m from the nest, they did not elicit a response from the incubating adult ($X^2 = 30.22$, df = 2, p <0.01). Incubating adult encounters with species in the no threat group elicited all three types of

responses. Any predator species that encountered nests less than five times were not included in

the analyses. The calculated risks of each of the predator species resulted in coyotes having the

highest level of risk relative to any of the other predator species, followed by crows, and ghost

crabs (Table 6).

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DISCUSSION

Wilson's Plovers on Cumberland Island National Seashore face a diverse assemblage of predators and nest threats. Three different survey methods (transects, searches of nest sites, and game cameras) produced similar estimates of the relative abundance of predators (Table 5). Only a small proportion of the predator assemblage, mainly coyotes and crows, caused the majority of Wilson's Plover nest failures. An increase in coyote predation may have caused a decrease in plover nest survival rates from 2014 to 2015. Abundance and distribution of the pervasive ghost crab had no detectable effect on the placement of plover nests or plover nest survival rates. Finally, male and female Wilson's Plovers encounter somewhat different predation threats (Figure 18), and plovers display different anti-predator behaviors based on the predator or threat approaching the nest (Figure 19).

As expected for a ground-nesting shorebird, I found that Wilson's Plovers are exposed to a diverse assemblage of mammalian and avian predators. In other shorebird studies, mammals (such as raccoons, bobcats and Virginia opossums), ghost crabs, and avian predators have also been shown to be responsible for the majority of the nest failures (Table 7; Corbat 1990, Sabine 2005, Ray 2011, Cox 2015). My results also agree well with other Wilson's Plovers studies that show most nest failures are caused by apex mammalian predators, mid-sized mammalian predators, or avian predators (Bergstrom 1982, Corbat 1990, Ray 2011, Cox 2015). In at least two studies on Wilson's Plovers, trampling by large mammals caused at least one nest failure (Bergstrom 1982, Corbat 1990), and two other studies noted that ghost crabs caused at least some nest failures (Ray 2011, Cox 2015). Of the studies conducted along the Georgia coast, only one other study identified coyotes as the major predator (Cox 2015).

One important finding of my study (and Cox's [2015] recent study) is that the major predator of Wilson's Plover nests seems to have changed over time (Table 7). Over the four consecutive years that predation was monitored at this study site, only seven out of 268 total nests, less than two percent of nests, were depredated by raccoons (Table 7, this study; Cox 2015). This number is extremely low compared to studies in other areas that found raccoons to be one of the primary shorebird nest predators on the east coast (Corbat 1990, Ray 2011). Even a study conducted in 2005 on CINS found that raccoons were the primary cause of nest loss (Sabine 2005). Coyotes, though causing a large number of nest failures, may be reducing the effects of other predators on the plover population on CINS. The key question is whether coyotes are a novel and additive source of predation for Wilson's Plovers, or coyote predation is compensatory because they reduce effects of other major predators such as raccoons.

If coyote predation were additive, I would expect to see increased predation rates, but with raccoons still causing approximately 18 percent of the nest failures (Corbat 1990). However, raccoon caused approximately 8 percent of the nest failures in 2014, and none in 2015. Thus, coyote predation on Wilson's Plover nests is most likely compensatory. If so, removal of coyotes could lead to mesopredator release (Goodrich and Buskirk 1995, Crooks and Soule 1999), with raccoons again becoming a major source of nest loss. Nevertheless, due to the high levels of nest predation on both sea turtle and shorebird nests by coyotes, removal of coyotes was implemented on CINS in June 2015. Only two weeks of the plover breeding season were left, so the nest success of plovers in 2015 was not affected by the removal of coyotes. The results of my study lead to the prediction that continued removal of coyotes will lead to increased nest predation by raccoons. This prediction should be tested in subsequent years.

To precisely quantify the predator assemblage impacting Wilson's Plovers would require extensive trapping and/or observation (Sanders and Maloney 2002). However, I found track surveys and game cameras to be viable methods to estimate the relative abundance of predators. The different techniques I used to determine predator presence generally described the same rank abundance of predators throughout my study site. A similar activity index was accurate in describing relative abundance for coyotes, white-tailed deer, and bobcats in southern Texas (Engeman et al. 2000).Track-count indices have also been used to monitor the activity of dingoes and Ethiopian wolves (Allen et al. 1996, Evangelista et al. 2009).

Because the different techniques described nearly the same assemblages of predators, I can compare the costs to get that information for each methodology. Using tracks as a means to identify predators is inexpensive (no equipment needed), but it requires a large effort in the field. Given the fleeting nature of tracks in a sandy environment, transect surveys or nest-site surveys need to occur on a regular basis (at least every 4-7 days). Game cameras need to be checked less frequently (every 6-9 days). Presumably the accuracy of track surveys would increase with even more frequent sampling. Regardless of the frequency of track surveys, they are simply an index of predator activity and they detect some species more readily than others (e.g., mammals vs. avian predators). Game cameras have higher precision and can be checked less frequently, but they are expensive (over $600 each), and they require stakes and mounts to secure them in sandy, coastal environments.

Cameras have a cost and a benefit that are particularly important to consider. The cost is that predators can learn to associate cameras with a nest. In 2015, a pair of crows learned to associate of one of the game cameras with the presence of a plover nest. When I suspected this, I moved the game camera to a random location away from active plover nests. The crows were

photographed approaching the camera multiple times over the next few days, presumably searching for a nest. The pair consumed eggs from four nests before I recognized the problem. I then removed all game cameras from the study site to prevent further incidents. However, a major benefit of cameras is that they produce an actual record of the activity at the nest. Game cameras confirm which predators consume the eggs, but they can also confirm how often that species and any other species are present near the nest site.

I found that predator encounters at a plover nest do not always result in nest failure. Coyotes and crows depredated nests in approximately 50% of their total encounters. This contrasts with Cox (2015), who found coyotes caused failures in 100% of the encounters. However, both studies agree that coyotes are a very high risk per encounter. This is not true of other predators or threats. For example, when trample threats such as horses approached within 3 m, they cause nest failures in only 2% of encounters (Figure 12). Ultimately, Wilson's Plovers experience a relative high number of encounters with potential predators at the nest (Figure 12), most which do not result in loss of the nest.

Although I captured evidence that ghost crabs take plover eggs, I attributed only two nest failures to them as the primary predator (Figure 20). In other studies, ghost crabs are attributed approximately the same proportion of nest failures (Ray 2011, Cox 2015). Therefore, I could not classify them as a major nest predator of Wilson's Plover. Piping Plover are similar, with frequent responses to ghost crabs but few nest failures attributed to ghost crabs (Wolcott and Wolcott 1999). Despite the fact that ghost crabs share habitat with Wilson's Plovers and elicit defense behavior in plovers, their distribution along the beach did not affect the placement of nests by Wilson's Plovers. In particular, during the first five weeks of the breeding season, there were more ghost crab burrows present in nest sites than in the randomly placed transects. This

supports the suggestion that plovers do not place their nests in areas with fewer ghost crabs. The only area of the study site with slightly higher ghost crab presence was also the section with the fewest breeding pairs of Wilson's Plovers. However, the lower number of breeding pairs could be due to factors other than the higher abundance of ghost crabs (Wolcott and Wolcott 1999).

The predator approaching the nest influenced the anti-predator behavior displayed, suggesting that Wilson's Plovers can recognize different species of predators or threats. Overall, a pattern emerged of plovers fleeing larger mammalian carnivores and defending against any other predator that posed some risk to the nest (Figure 21, Figure 22). The risk of the predator to the adult could be the key in whether the adult flees or defends the nest. For example, coyotes pose a high risk to the eggs per encounter, yet the incubating adults flee. This is probably because adult Wilson's Plovers will renest. Therefore, defending the eggs from a dangerous coyote may not be worth the risk. Similar reasoning probably explains why age of clutch does not affect the responses displayed by incubating adults in my study and in Two-banded Plover (St. Clair et al. 2010a). Because Wilson's Plovers will lay multiple clutches in a season, and nest for multiple years, lack of a fine-tuned response to investment in a single clutch is probably not surprising.

One variable that should be tested in the future is the effect that the renesting potential has on the anti-predator behavior displayed by Wilson's Plovers. Because relatively few breeding adults are banded at my study site, I could not confirm how many clutches each pair produced. Models suggest that the potential to renest will decrease the intensity of anti-predator displays shown by incubating adults (Montgomerie and Weatherhead 1988). The ability of Wilson's Plovers to renest each season and each year could cause some of the currently unexplainable variation found in the behavior I observed. In some territories in my study site, I

estimated one pair could have renested up to four times in a single breeding season. If plovers regularly renest that often in a single breeding season, defense intensity could vary based on which nest attempt the incubating adults (e.g. first nest of the season or the fourth nest of the season). It could explain why I saw differences in my analyses such as some adults reacting strongly to species that posed low risk to the nest, or why other adults did not react to trample threats within 3 m of their nest.

Males and females respond to predators differently (Figure 15). However, because the sexes incubate at different times of day, they also are exposed to different predators (Figure 18). Dangerous predators like coyotes are encountered almost exclusively by males, whereas avian predators like crows are encountered almost exclusively by females. Thus, it is difficult to assess whether male and female Wilson's Plovers show inherent differences in response to predators. Two-banded Plovers (*Charadrius falklandicus*) show no sex-based differences in their anti-predator behavior (St. Clair et al. 2010b). An experimental approach will probably be required to resolve this question in Wilson's Plovers (see below).

There was a slight decrease in the survival of nests with males incubating than with females incubating. However, this could be due to the different assemblage of predators each sex encounters. Because a higher proportion of males encountered coyotes than females, males lost a larger proportion of the nests to depredation by coyotes than females. Sabine (2005) found that a larger proportion of American Oystercatcher nests failed at night than during the day, which supports that the different assemblage of predators seen by adults at night could be the cause of the higher nest failure rate. Apex mammalian predators and mid-sized mammals, the major nest predators of shorebirds, are primarily nocturnal or crepuscular and cause nest failures more frequently at night (Sabine 2005).

To better understand how the sexes of Wilson's Plovers respond to different predators, an experimental approach is called for (Altmann 1974). I did stage encounters with predator models with some success. However, most of the simulated predator encounters were unsuccessful. Simulated predator experiments failed for two reasons. First, many adult Wilson's Plovers were extraordinarily sensitive to the blind. Despite prolonged waiting periods, adults would not return to normal activity. One solution was to leave the empty blind out overnight so that plovers could acclimate. However, its presence then attracted the attention of coyotes. A second problem was the inability to make the artificial predator approach the nest. Originally I used a remote-controlled motorized vehicle hidden by canvas with the artificial predator attached, but the vehicle would not move in soft sand. I then used a rope system to simulate the artificial predator approaching the nest, but the soft sand was still a problem. I switched to an immobile predator hidden under canvas within 3 m of the nest, but the adults were too sensitive to the blind presence to fully test this method.

In future studies, the blind should not be placed closer than 20 m from the nest and should be left overnight prior to running the experiment, if possible. The ability to move the artificial predator was an important part of this study that should be considered. Because there was a difference in the reactions in trample threat distances from the nests, there could be a difference in the reaction shown by incubating adults with the different distances of other predators as well. During the day, I was able to more easily determine in the game camera photos the predator distances from the nest. At night, the infrared photo capture on the game cameras was limited in the distance it could capture. Unfortunately, this made it more difficult to determine the distances of the predators to the nests at night. Using artificial predators that can move through soft sand would help determine if the distance of the predator from the nest

changes how the plover reacts to the predator. It would also determine if there are differences in the display rates of males and females, or if the display rates are due to other factors such as the assemblage of predators that each sex encounter most frequently or the time of day that the encounter occurs.

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Table 1. Frequency (and percent) of Wilson's Plover nests destroyed by different species of predators or threats in 2014 and 2015. Species that caused no known failures are listed for comparison with relative abundance data.

Predator	Total	2014	2015
Unknown	38 (47.50%)	8 (34.78%)	30 (52.63%)
Coyote	25 (31.25%)	6 (26.08%)	19 (33.34%)
Crow	10 (12.50%)	3 (13.04%)	7 (12.28%)
Ghost Crab	2 (2.50%)	2 (8.70%)	0 (0%)
Feral Horse	2 (2.50%)	1 (4.35%)	1 (1.75%)
Raccoon	2 (2.50%)	2 (8.70%)	0 (0.00%)
Bobcat	1 (1.25%)	1 (4.35%)	0 (0.00%)
Nine-banded Armadillo	0 (0.00%)	0 (0.00%)	0 (0.00%)
White-tailed Deer	0 (0.00%)	0 (0.00%)	0 (0.00%)
Feral Pig	0 (0.00%)	0 (0.00%)	0 (0.00%)
Virginia Opossum	0 (0.00%)	0 (0.00%)	0 (0.00%)
Total	80	23	57

Table 2. Number of transects on which each predator was detected in 2015. Relative abundance is the mean number of track crossings per 100 m of transects averaged by transect (N = 32).

Predator	Number of transects (percent)	Relative abundance (per 100 m) ± SE
Ghost Crab	32 (100%)	30.06 ± 2.14
Coyote	31 (97%)	1.09 ± 0.13
Feral Horse	18 (56%)	3.49 ± 0.40
Nine-banded Armadillo	12 (38%)	1.27 ± 0.13
White-tailed Deer	3 (9%)	0.41 ± 0.02
Feral Pig	2 (6%)	0.99 ± 0.04
Crow	1 (3%)	0.89 ± 0.03
Raccoon	1 (3%)	0.37 ± 0.01
Bobcat	0 (0%)	0.00 ± 0.00
Virginia Opossum	0 (0%)	0.00 ± 0.00

Table 3. Number (and percent) of nest sites (10-m radius) in which each species of predator was detected. A total of 63 nests sites were sampled in 2014 and 73 in 2015.

Predator	Total	2014	2015
Ghost Crab	134 (99%)	63 (100%)	71 (97%)
Coyote	76 (56%)	26 (41%)	50 (68%)
Feral Horse	101 (74%)	60 (95%)	38 (52%)
Nine-banded Armadillo	19 (14%)	3 (5%)	16 (22%)
White-tailed Deer	48 (35%)	16 (25%)	32 (44%)
Feral Pig	9 (7%)	6 (10%)	3 (4%)
Crow	34 (25%)	13 (21%)	21 (29%)
Raccoon	18 (13%)	13 (21%)	5 (7%)
Bobcat	4 (3%)	4 (6%)	0 (0%)
Virginia Opossum	1 (1%)	1 (2%)	0 (0%)

Table 4. The number (and percent) of nests with game cameras that each species of predator or threat were present throughout the study site. In 2014, 19 nests had game cameras placed at them for all or a portion of their incubation. In 2015, 26 nests had game cameras placed at them for all or a portion of their incubation. (N = 45)

Predator	Total	2014	2015
Ghost Crab	15 (33%)	9 (47%)	6 (23%)
Coyote	16 (36%)	5 (26%)	11 (42%)
Feral Horse	19 (42%)	7 (37%)	12 (46%)
Nine-banded Armadillo	3 (7%)	1 (5%)	2 (8%)
White-tailed Deer	10 (22%)	6 (32%)	4 (15%)
Feral Pig	1 (2%)	1 (5%)	0 (0%)
Crow	13 (29%)	7 (37%)	5 (19%)
Raccoon	0 (0%)	0 (0%)	0 (0%)
Bobcat	0 (0%)	0 (0%)	0 (0%)
Virginia Opossum	2 (4%)	2 (10%)	0 (0%)

Table 5. Comparison of predators detected by the three survey methods. Numbers are the percent of transects, nest sites (10-m radius), and encounters at nest photographed by cameras at which a given species was detected. Rank of frequencies are given in parentheses.

Predator	Transects	Nest Sites	Game Cameras
Ghost Crab	100 (1)	99 (1)	33 (3)
Coyote	97 (2)	56 (3)	36 (2)
Feral Horse	56 (3)	74 (2)	42 (1)
Nine-banded Armadillo	38 (4)	14 (6)	7 (6)
White-tailed Deer	9 (5)	35 (4)	22 (5)
Feral Pig	6 (6)	7 (8)	2 (8)
Crow	3 (7)	25 (5)	29 (4)
Raccoon	3 (7)	13 (7)	0 (9)
Bobcat	0 (8)	3 (9)	0 (9)
Virginia Opossum	0 (8)	1 (10)	4 (7)

Table 6. Relative risk to Wilson's Plover nest survival as a function of the predators found in the nest sites multiplied by the odds of those predators causing a nest failure.

Predator	Frequency in the nest sites	Frequency of species' presence causing a nest failure	Relative Risk
Ghost Crab	0.99	0.11	0.11
Coyote	0.56	0.50	0.28
Feral Horse	0.74	0.02	0.01
Nine-banded Armadillo	0.14	0.00	0.00
White-tailed Deer	0.35	0.00	0.00
Feral Pig	0.07	0.00	0.00
Crow	0.25	0.53	0.13
Raccoon	0.13	0.00	0.00
Bobcat	0.03	0.00	0.00
Virginia Opossum	0.01	0.00	0.00

Table 7. Comparison of the top predator in this study to top predator found in other studies of shorebird nest success. Predator classifications listed are those used in each of the studies. Percent of nest failure caused by each predator is the percent of all failed nests in each study.

Reference	Species	Year(s)	Location	Major Predator	Other predators
Bergstrom 1982	Wilson's Plover	1980	Texas	Coyote (19%)	Jaguarundi (*Puma yagouaroundi*), Cattle
Corbat 1990	American Oystercatcher	1986-1987	Georgia	Raccoon (18%)	Feral pig, Avian, Cattle
Corbat 1990	Wilson's Plover	1986-1987	Georgia	Raccoon (18%)	Avian, Mammal, Feral pig, Trampling
Corbat 1990	Least Tern	1986-1987	Georgia	Raccoon (37%)	Ghost crab
Sabine 2005	American Oystercatcher	2003-2004	Georgia	Raccoon (39%)	Bobcat, Crow, Trampling, Humans
Ray 2011	Wilson's Plover	2008-2009	North Carolina	Virginia Opossum (29%)	Raccoons, Ghost crabs, Rodents
Cox 2015	Wilson's Plover	2012-2013	Georgia	Coyote (16%)	Raccoons, Ghost crabs, Deer, Feral pig, Crow
Current Study	Wilson's Plover	2014-2015	Georgia	Coyote (26%)	Crow, Raccoons, Ghost crabs, Trampling, Bobcat

Figure 1. Cumberland Island National Seashore, Georgia, with the 7-km study site indicated by the gray bar.
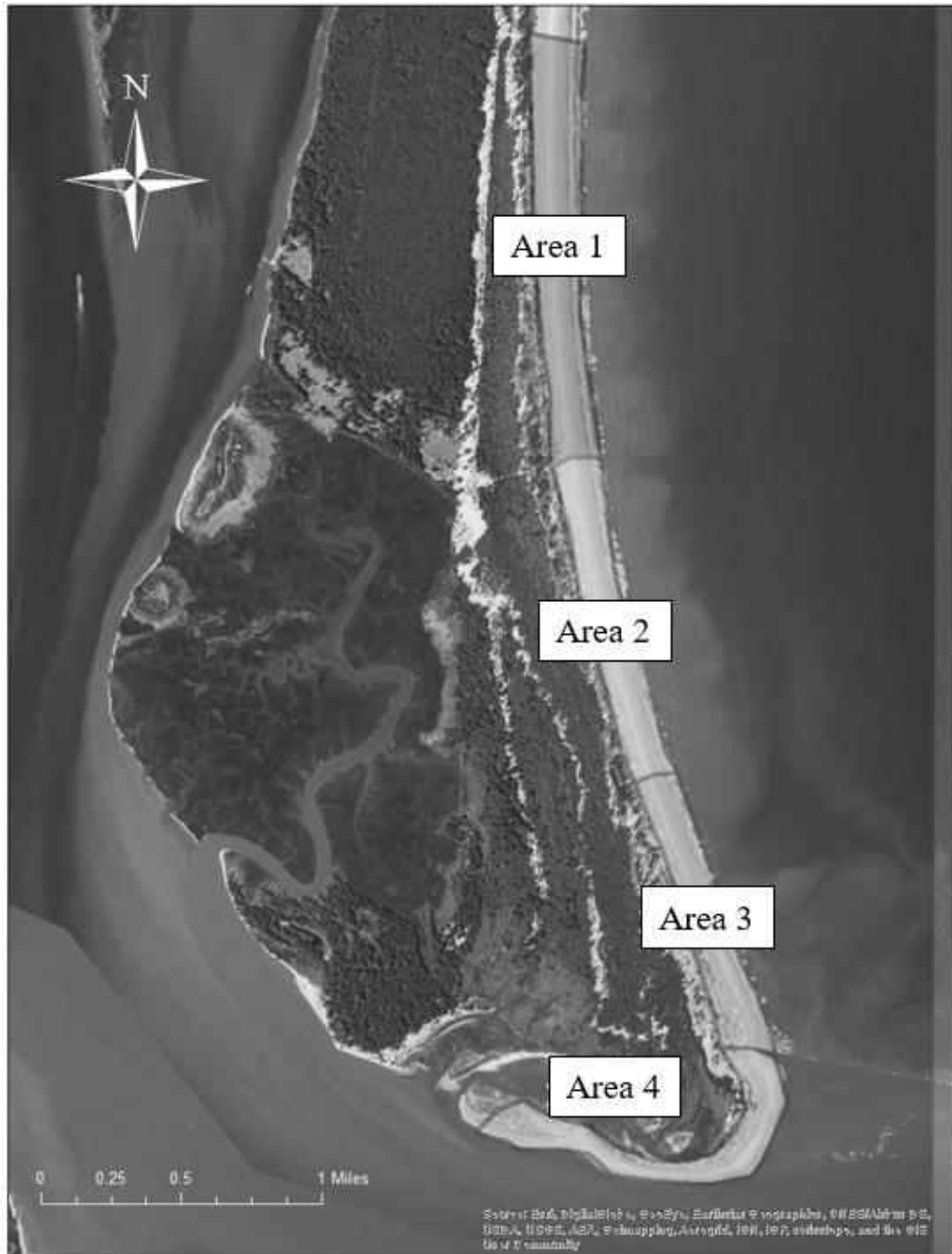
Figure 2. The study site was divided into four distinct areas. Area 1 was an area with higher levels of human foot traffic and lower Wilson's Plover densities. Area 2 had less human foot traffic and a higher density of Wilson's Plovers. Area 3 had the least human foot traffic and the lowest density of Wilson's Plovers. Area 4 was an area where boaters can beach their boats, so the human traffic was high, but the plover density was highest in this area.
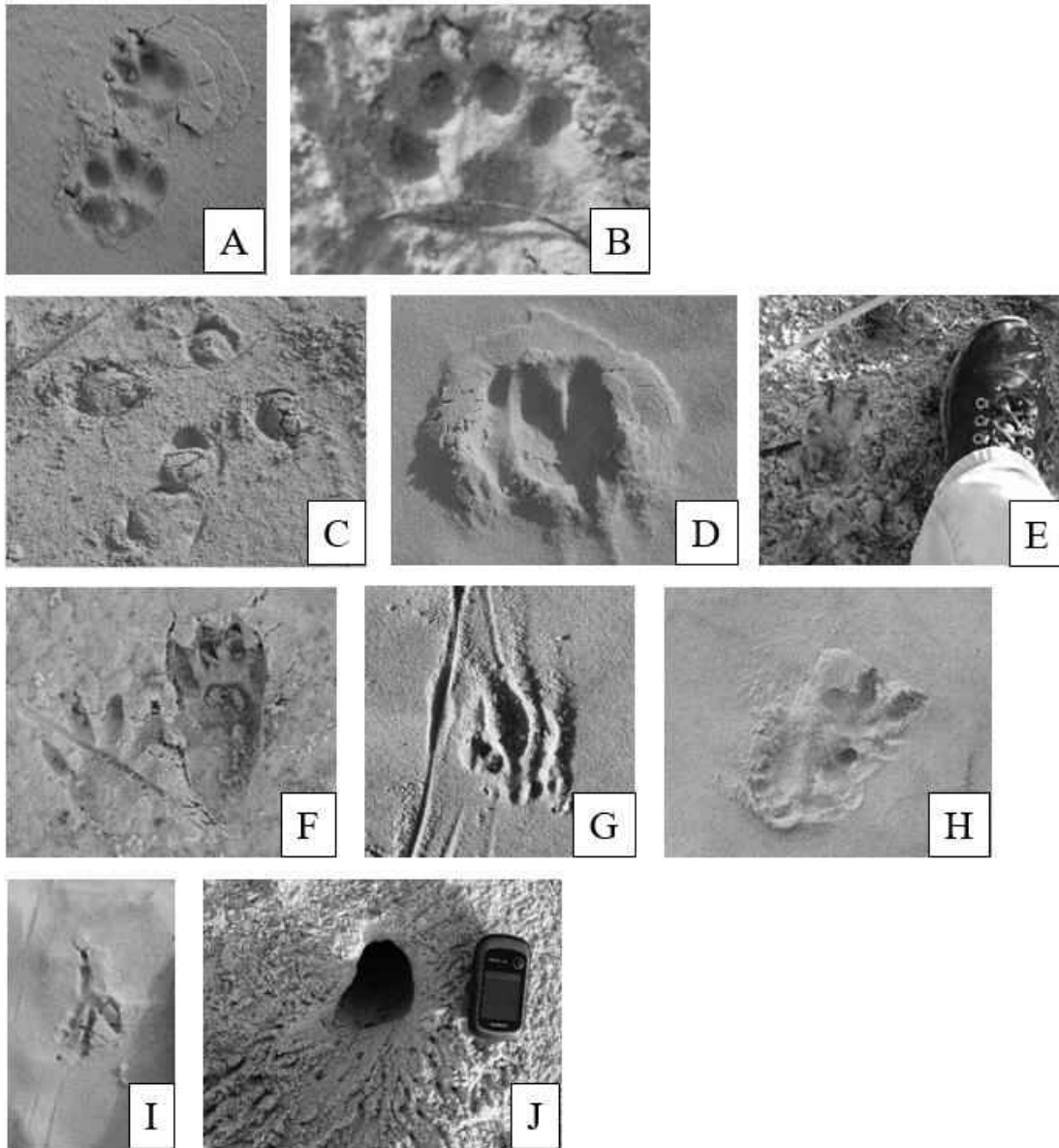
Figure 3. Examples of predator tracks identified. (A) coyote, (B) bobcat, (C) feral horse, (D) white-tailed deer, (E) feral pig, (F) raccoon, (G) nine-banded armadillo, (H) Virginia opossum, (I) crow, (J) ghost crab burrow.

Figure 4. Locations of the 32 predator transects.

Figure 5. Nest locations throughout the study site for both the 2014 and 2015 breeding seasons. I located 63 nests in 2014 and 73 nests in 2015.

Figure 6. Nest fate for all nests on the study site in 2014 and 2015.

Figure 7. Causes of failure for the 95 failed nests indicated in Figure 6.

Figure 8. Predators responsible for failures due to predation indicated in Figure 7.
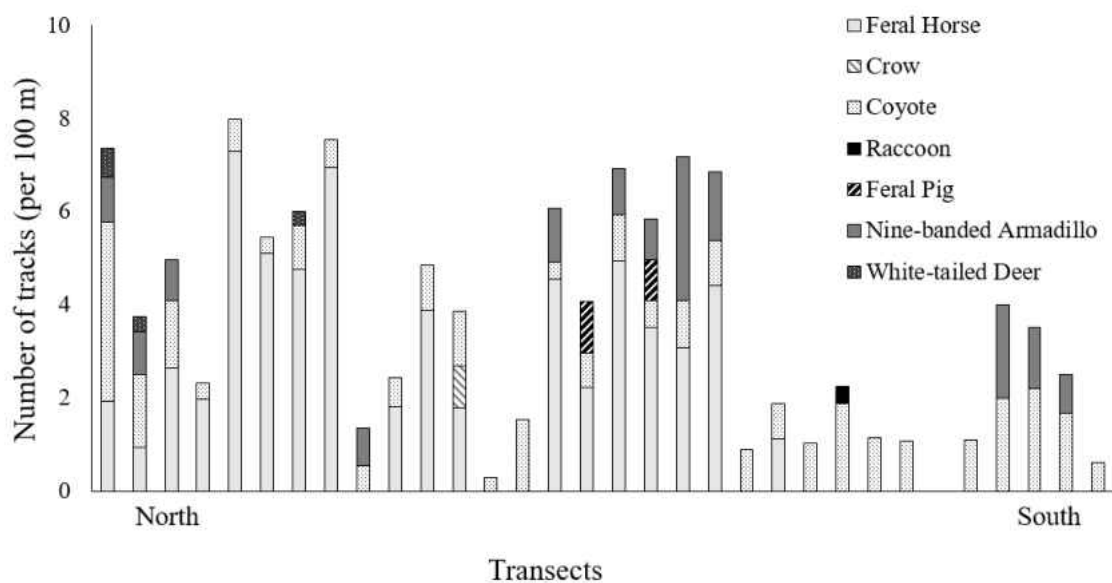
Figure 9. Mean number of tracks (per 100 m) found on each transect for each predator detected. Transects are shown in order from the north to the south ends of the study site (see Figure 4).
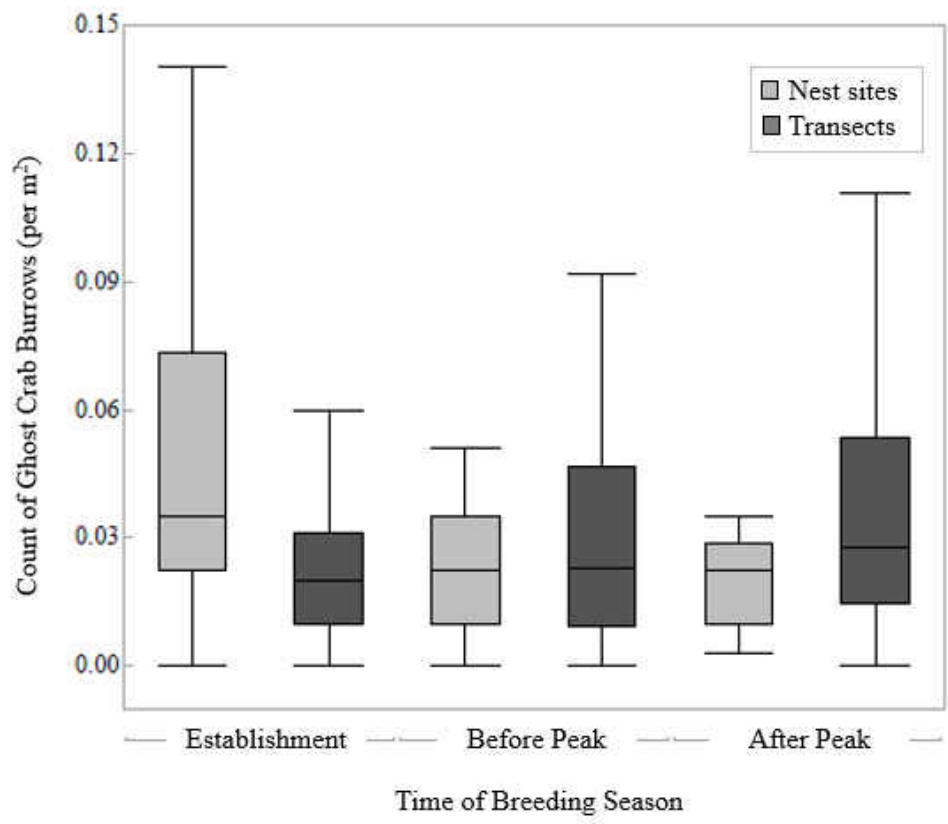
Figure 10. The count of ghost crab burrows per m^2 found in the nest sites and transects in the three periods of the breeding season. The establishment period consists of the first five weeks of the breeding season, the before peak period consisted of the next five weeks, and the after peak period consisted of every week after the before peak period until the end of the incubation of the final surviving nest.
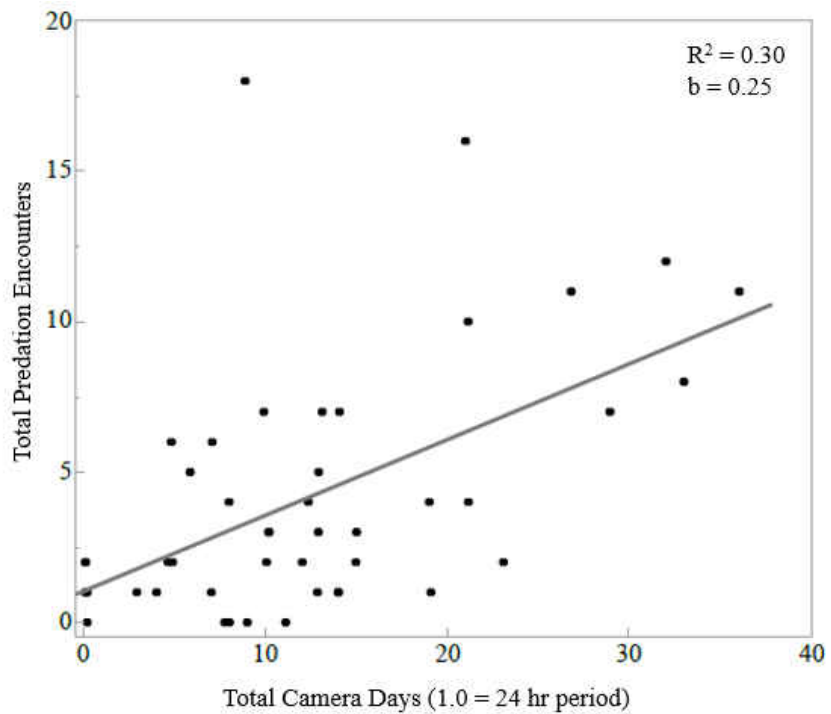
Figure 11. Relationship of predation events at Wilson's Plover nests to number of days camera was deployed.
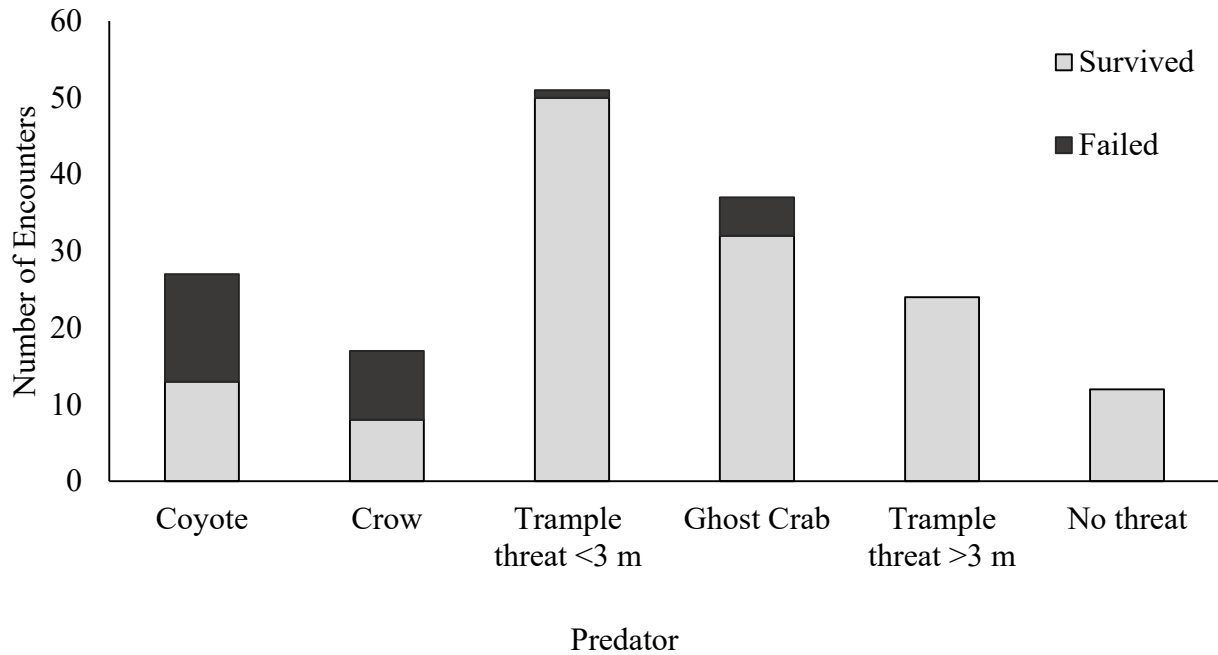
Figure 12. The total number of encounters captured at plover nests by each predator species or threat group and the outcome of each of those encounters. Feral horses and white-tailed deer comprise the trample threat groups, and were classified as farther than 3 m from the nest (>3 m) or within 3 m of the nest (<3 m). The no threat group was comprised of species not considered threats to the incubating adults or the nests such as Mourning Doves, Willets, Wild Turkeys, and Savannah Sparrows. (N = 45; X^2 = 51.91, df = 5, p <0.01).
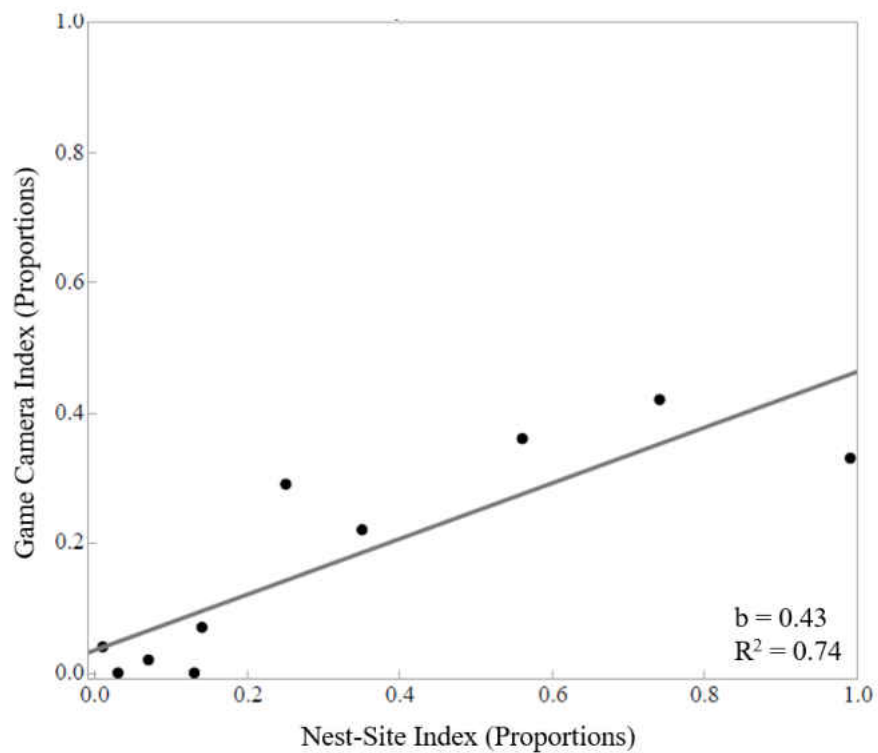
Figure 13. Relationship between predator relative abundance indicted by cameras to that estimated by nest-site surveys. N = 136 nest-sites and 45 camera sites.
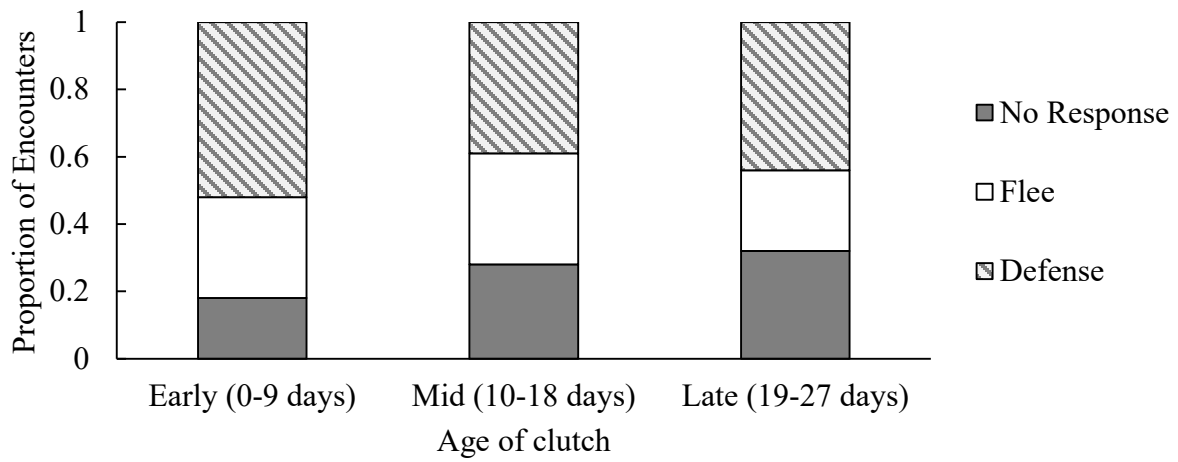
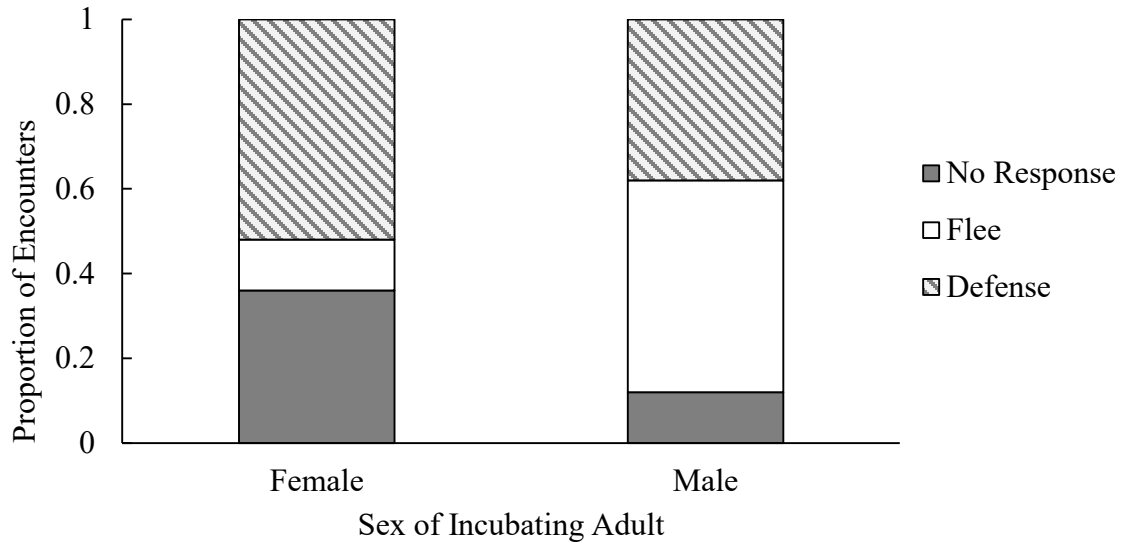Figure 14. Response of adult plovers to potential predators as a function of clutch age.

Figure 15. Response of adult plovers to potential predators as a function of sex.
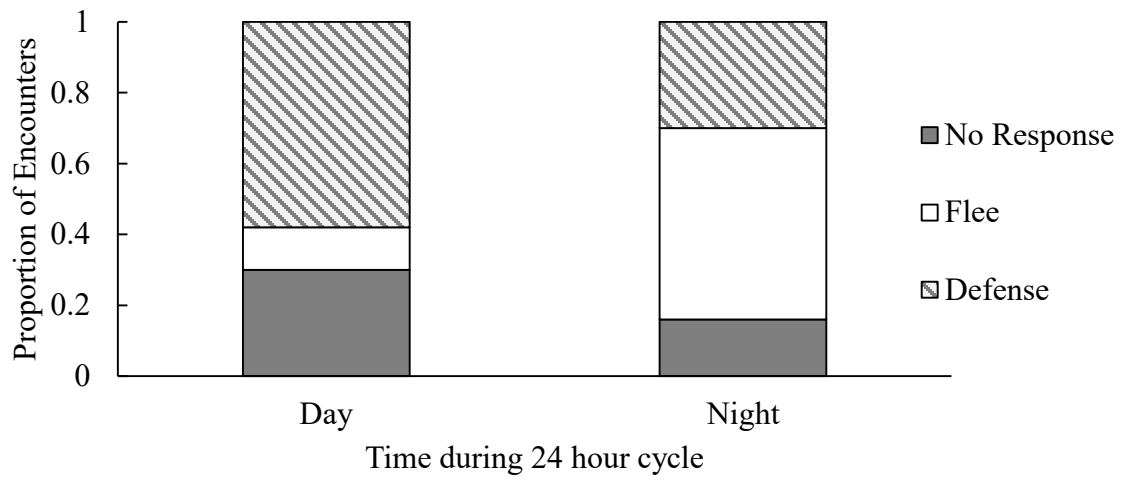
Figure 16. Response of adult plovers to potential predators as a function of time of day.
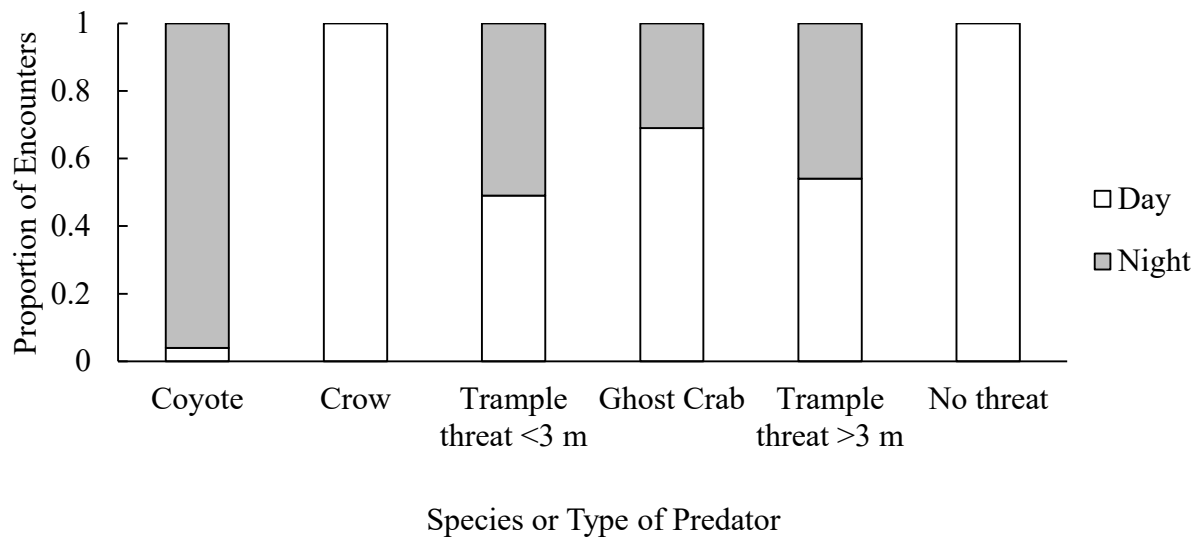
Figure 17. Proportion of predator encounters captured on game cameras by each predator species as a function of time of day.
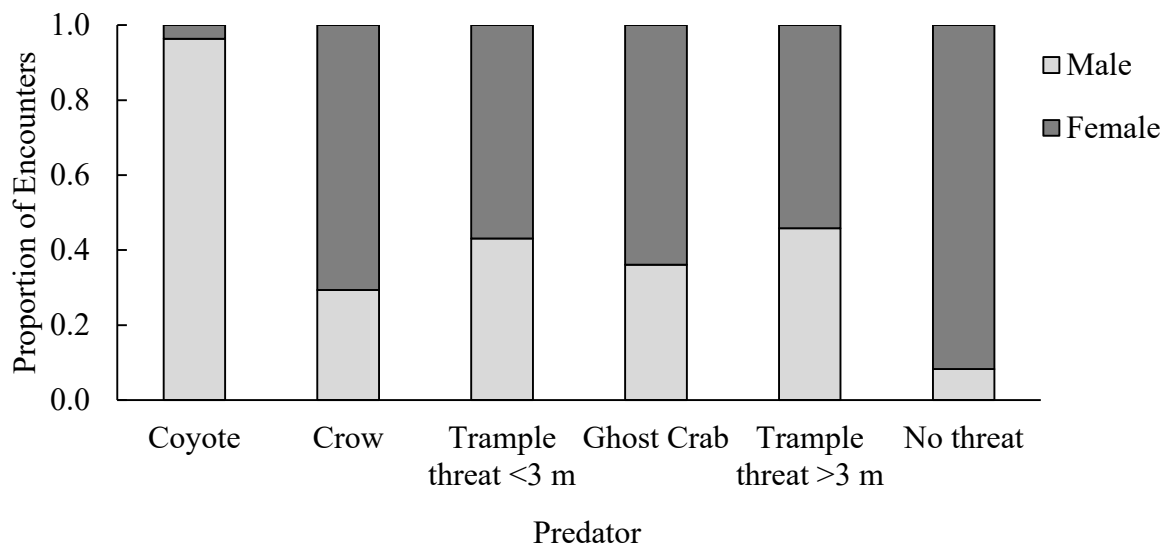
Figure 18. Potential predators encountered by male and female Wilson's Plovers.
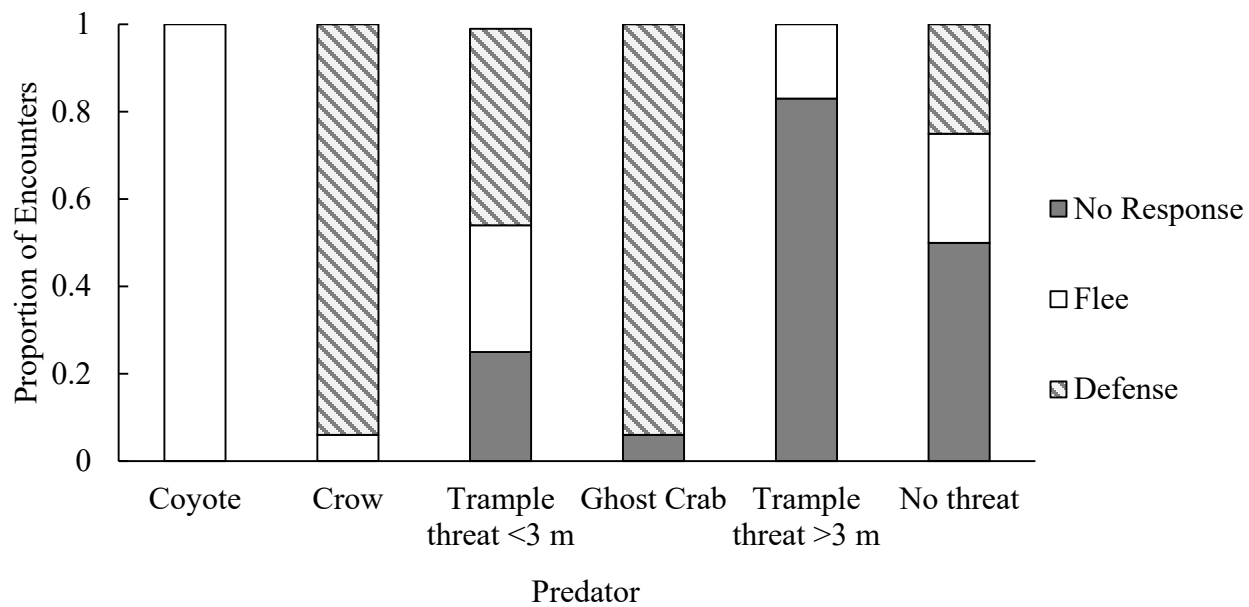
Figure 19. Responses of adult plovers to different potential predators.

Figure 20. Evidence of a ghost crab removing and eating a Wilson's Plover egg from a nest, July 6, 2014, at 10:10 am on Cumberland Island National Seashore, GA.

Figure 21. A female Wilson's Plover reacting in defense to a feral horse that had approached within 3 m of the nest she was incubating. The photo was taken on March 31, 2015, at 6:36 pm. This was the typical spread-wing display against a predator that poses risk to the nest, but poses little to no risk to the adult.

Figure 22. A female Wilson's Plover responding to a ghost crab near the eggs she was incubating. The photo was taken on May 8, 2015, at 9:18 am. This was the typical spread-wing display against a predator that poses risk to the nest, but poses little to no risk to the adult.