CONSERVATION AND MANGEMENT OF THE SNOWY PLOVER ALONG THE FLORIDA GULF COAST: HABITAT SELECTION AND THE CONSEQUENT REPRODUCTIVE PERFORMANCE

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2010

To my Grandma Francis
who passed away during this study, but in life inspired me in her passion for birds

ACKNOWLEDGMENTS

I am grateful to Marvin Friel for his dedication, support, and assistance to this project in and out of the field. I thank my two dogs (Mazzy and Snowy) who were extraordinarily patient and understanding of the long hours I spent in the field. I thank my family who always encouraged me to follow my passions while stressing the importance of education. I am indebted to my advisers Steve Johnson and Rob Fletcher for providing me with this opportunity and for invaluable guidance and input during this study. I also thank my remaining committee member Debra Miller, for her interest and guidance particularly in detailing methods for tracking in coastal habitats. I have had many valuable and interesting discussions with my lab ‘space’ mates in addition to my fellow graduate students in the WEC department, and I am appreciative for their assistance and friendship. I am very grateful to Patty Kelly with the U.S. Fish and Wildlife Service for providing financial support for this study. Thanks also to Rich Fischer with the Corp of Engineers for additional financial support. I would like to thank Janell Brush, John Himes, Shea Armstrong, Jeff Gore, and Chris Paxton with the Florida Fish and Wildlife Conservation Commission (FWC) for providing much needed equipment and support. I would like to thank the Department of Environmental Protection (Florida State Parks) staff at both the Northwest regional office and St. Joseph State Park, particularly Harold Mitchell, Jared Zimmerman, Joe Mitchell, and Brian Addison. I would like to thank Wendy Jones and the remaining natural resource staff at Tyndall Air Force Base. Thanks also to the staff at St. Vincent National Wildlife Refuge for providing access to and from the island for surveys. I am thankful to Steve Shea and Bill Lynn with the St. Joe Company for allowing me access to their properties. Barbara Eells, a volunteer with the St. Joe Company, provided invaluable assistance, support and friendship for which I am very grateful. I would also like to thank John Andrews and Elisa Martinez for assistance with data entry.

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May 2010

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Major: Wildlife Ecology and Conservation

To expand upon the current ecological knowledge of Snowy Plovers, I studied breeding Snowy Plovers nesting along the Florida panhandle during 2008-09. I contrasted four alternative hypotheses (prey availability, human activity, predator activity, and physical features of the habitat) and the influence each had on habitat selection and reproductive performance during both the nesting and brood-rearing stages of breeding. I modeled the probability of selection and the daily survival rates as a function of predictors representing each hypothesis by breeding stage (i.e., nesting, brood-rearing). Nest-site selection and daily nest survival were a function of all four hypotheses working in combination. In contrast, brood-site selection was a function of prey availability alone and daily brood survival was a function of prey availability, predator activity, and physical features combined. Collectively, this information will provide for habitat management that will benefit the Snowy Plover. Additionally, my results provide a unique demonstration of how multiple selective forces influence site selection and reproductive performance that is relevant to wildlife in general.

CHAPTER 1
INTRODUCTION

Few species are evenly or randomly distributed within or across landscapes. In general, the distribution of wildlife species significantly varies across the landscape in association with environmental features that influence their reproductive success and population persistence (Martin 1998; Groom et al. 2006). However, species' distributions do not consistently parallel those predicted by the availability of suitable habitat features (Nelson 2007). Studies quantifying the habitat selection process and the fitness consequence for a given species can address these inconsistencies in predictability and provide potential mechanisms for patchy distributions.

Selection of breeding habitat is an important decision for many species (Rosenzweig 1991). Habitat selection refers to behavioral responses that result in the disproportionate use of habitats and/or resources that presumably improve survival of individuals (Thomas and Taylor 1990; Block and Brennan 1993). Obtaining data on habitat selection and the subsequent reproductive fitness consequences allows for ascertaining habitat quality, which is defined as the ability of the habitat to sustain life and support population growth (Garshelis 2000; Colwell et al. 2005). Understanding habitat selection behavior augments the potential for proper management by informing practitioners of the cues animals' likely use when deciding whether or not to occupy a habitat.

Coastal Animal Communities - Coastal Habitat

Coastal habitats are naturally dynamic and harsh environments. The action of waves and tides largely determine the level of species diversity, biomass, and community structure (Brown and McLachlan 2002). Coastal habitats have received attention world-wide because they appear to be declining on a large spatial scale due to habitat alteration, recreational use, development and direct disturbance from people and pets (Chase and Gore 1989; Burger 2000; Lafferty 2001a; Lafferty 2001b). Current estimates of global population growth predict around 7.1 billion people by 2020 (United Nations 1998). Of the 7.1 billion people, 75% are predicted to live within 60 km of the coast (Roberts and Hawkins 1999), leading to increases in direct pressures to coastal environments and coastal-dependent species (Burger 2000). The greatest threat to coastal habitats is the serious erosion issues associated with human structures and activities that disrupt the transport of sand (Brown and McLachlan 2002). In Florida alone, 700 km of shoreline are threatened by severe erosion as a result of jetties, groins, and seawalls used to protect coastal development (Finkl 1996). Most often these structures are built to protect developed lands from the effects of storms (i.e. hurricanes) (Brown and McLachlan 2002), but they may also prevent the natural accretion of sand.

Habitat Selection Constraints

Recently, researchers and public land managers are interested in the influences related to rising sea-levels and anthropogenic alteration on the habitat selection process. Both have the potential to contribute to habitat loss to wildlife (Brown and McLachlan 2002), changes in predator communities including mesopredator release (Groom et al. 2006), and changes in foraging availability (Crooks 2004). All these effects can have dramatic consequences for population dynamics. In particular, these impacts could influence the habitat selection process in a number of ways, including altering the availability of habitat for individuals to chose from, influencing behavioral decision-rules animals use during habitat selection, or by altering the fitness consequences of habitat selection (e.g., Robertson and Hutto 2006).

Human Activity

Habitat alteration and loss of habitat has intensified the spatial overlap between wildlife and humans (Weston and Elgar 2007). An increase in human-wildlife contact alters use patterns within the landscape by excluding individuals from potential habitat (Gill et al. 2001; Stillman 2003). Consequently, recreational activities are a central cause of population declines in many species listed as federally threatened or endangered (Czech et al. 2000). For example, tourism has resulted in increased recreational pressures on coastal habitats and has contributed to global declines in coastal-dependent species, particularly shorebirds (Burger 2000; Gill et al. 2001; Lord et al. 2001; Ruhlen et al. 2003; Yasue and Dearden 2006a). Habitats that appear to be intact can lose value to wildlife when human activities interfere with behaviors such as foraging (Lord et al. 1997), roosting (Lafferty et al. 2006), and breeding (Yasue and Dearden 2006a). Interests in the effects of human disturbance has increased in recent years (Burger 2000; Gill et al. 2001; Lord et al. 2001; Ruhlen et al. 2003, Lafferty et al. 2006; McCrary and Pierson 2006; Yasue and Dearden 2006a) and have produced an array of contrasting conclusions and as a result our knowledge of impacts to wildlife associated with human disturbance are limited.

Prey Availability

For most species food availability is arguably the single most important determinant for patterns of selection and species occurrences in natural communities (Frederick et al. 1996; Granadeiro et al. 2004) due to energy requirements associated with both reproduction and survival (Schekkerman and Visser 2001). Consequently, changes in prey abundance have the ability to alter usage patterns as well as species settlement patterns within landscapes (Evans and Dugan 1984; Goss-Custard 1984). These patterns are particularly important for species with precocial young (e.g. shorebirds, waterfowl). Precocial offspring must have access to a reliable food supply because the collection of necessary food is shifted to the chick (Schekkerman and Visser 2001). Thus, food requirements likely influence both nest and brood foraging-site selection for precocial species. In fact, research on coastal invertebrates in relation to shorebird habitat use suggests that it is possible for prey abundance to be high enough to compensate for negative human impacts (Gill et al. 2001; Smith and Faillace 2006; Finn et al. 2007).

Predation

Avian species are generally vulnerable to predation (Martin 1995). In fact, chronically low reproductive rates have been identified as a major cause for population declines for many avian species (Martin 1998; Colwell et al. 2005). Many avian species are influenced by density dependent predation (Schmidt and Whelan 1999). Consequently the maintenance of low nesting density is an important anti-predator adaptation for many bird species (Page et al. 1983). However, habitat loss has the potential to increase conspecific nest density resulting in increased predation pressures (Himes et al. 2007). In addition to potential impacts due to density-dependence, predation pressure may increase due to mesopredators associated with human activity, particularly in relation to garbage (Lafferty 2001a; Groom et al. 2006). Thus, it is essential to determine predation rates and identify the types of predators that might be influencing nest success and recruitment.

Snowy Plover (*Charadrius alexandrinus*) in Florida

The Snowy Plover is one of the most imperiled bird species in the U.S. due to its patchy distribution and wide-spread loss of habitat (Gorman and Haig 2002; Funk et al. 2007). Although controversial (Gorman and Haig 2002; Funk et al. 2007), at least six morphologically distinct subspecies are recognized (O'Brien et al. 2006), two of which occur in North America. The Western Snowy Plover (*C. a. nivosus*) has migratory and non-migratory populations west of the Rocky Mountains. The Cuban Snowy Plover (*C. a. tenuirostris*) has migratory and non-migratory populations on the Gulf Coast of the U.S. from Louisiana east to Florida, and in the West Indies (Bennett and Wallace 2001). The Florida Fish and Wildlife Conservation Commission (FWC) has conducted three state-wide surveys over the past 21 years: 1989 (Chase and Gore 1989), 2002 (Lamonte et al. 2006), and 2006 (Himes et al. 2007). The most recent study documented 177 breeding pairs in Northwest Florida and 45 breeding pairs in Southwest Florida (Himes et al. 2007).

The Snowy Plover population in Florida is particularly vulnerable since it is restricted to barrier islands and a few coastal mainland beaches along the Gulf Coast, and it presumably functions as a demographically closed population (Funk et al. 2007). Threats to the Snowy Plover population in Florida include development of beachfront property, disturbance by people and pets, high predation rates, and habitat loss or degradation due to coastal engineering activities (Chase and Gore 1989; Gore 1996; Lamonte et al. 2006; Himes et al. 2007). Furthermore, the Snowy Plover breeding season begins in mid-February and lasts until the end of August, which overlaps with the tourism season (Chase and Gore 1989; Lamonte et al. 2006; Himes et al. 2007). Due to these threats, the Snowy Plover is listed as Threatened by the FWC (Florida

Administrative Code 68A-27.004) and as Endangered by the Florida Committee on Rare and Endangered Plants and Animals (Gore 1996). Additionally, *Charadrius a. tenuirostris* is currently considered a Candidate Species by the USFWS under the Endangered Species Act. Yet because of the lack of historic data on the Florida population, the demographic response to either habitat loss or alteration has not been documented.

The main predators observed during previous Snowy Plover surveys in Florida, included coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and ghost crabs (*Ocypode quadrata)* (Himes et al. 2007). Ghost crabs have also been observed directly predating upon Snowy Plover chicks (B. Eells, pers. comm.). In addition, fish crows (*Corvus ossifragus*) and laughing gulls (*Leucophaeus atricilla*) were observed taking Snowy Plover eggs (pers. Obs.) and chicks (B. Eells pers. comm.).

Project Objectives

Although many studies have demonstrated population declines due to predation (Page et al. 1983), others have demonstrated changes in habitat use and breeding success as a result of human disturbance (Burger and Gochfeld 1991; Ruhlen et al. 2003; Yasue and Dearden 2006a). However, most studies have examined disturbance in isolation from other ecological factors (Yasue and Dearden 2006a). Thus, there is a need to incorporate variables related to habitat use and selection including human disturbance, alteration of habitats, environmental factors, and potential predation (Gill et al. 2001; Stillman and Goss-Custard 2002; Yasue 2005). This allows for more accurate assessment of human disturbance and ecological factors that may affect breeding success (Frid and Dill 2002; Yasue 2005). In addition, the precocial life history of plover offspring necessitates not only understanding nest-site selection and success, but also the requirements of Snowy Plover broods. Given the high energy demands and high mortality of most shorebird chicks to either starvation or exposure (Pearce-Higgens and Yalden 2004), it is likely that habitat selection and diet are critical for their survival.

This study specifically focuses on identifying potential impacts to the Snowy Plover population with the goal of guiding management for the conservation of this species. Additionally, knowledge of the effects of anthropogenic alteration and the reproductive consequences lags far behind the growing global problem, yet such knowledge is essential for mitigating possible long-term effects.

CHAPTER 2
THE INFLUENCE OF HUMAN AND PREDATOR ACTIVITY, PREY AVAILABILITY AND PHYSICAL FEATURES OF THE HABITAT ON NEST-SITE SELECTION AND REPRODUCTIVE OUPUT, USING A SUBTROPICAL SHOREBIRD

Introduction

Habitat selection is fundamentally important to numerous issues in ecology and conservation (Martin 1998; Groom et al. 2006). Habitat selection refers to behavioral responses that result in the disproportionate use of habitats and/or resources that presumably improve survival and fitness of individuals (Thomas and Taylor 1990; Block and Brennan 1993). For example, in avian species the choice of nest site may determine the probability that predators will discover the offspring (Martin 1998). In selecting habitat, animals respond to environmental cues, which are environmental features that animals can observe at the time of choice (Williams and Nichols 1984). Potential influential cues include foraging sites, nesting sites, favorable microclimates, and places to avoid predators or competitors (Steele 1993). Understanding habitat selection behavior augments the potential for proper management by informing practitioners of the cues animals likely use when deciding whether or not to occupy a habitat.

While investigations on habitat selection have long focused on food, predators, and habitat features, the effects of anthropogenic disturbance are of increasing interest due to rapid growth of the human population. An increase in human-wildlife contact can alter use-patterns within the landscape by excluding individuals from locations that provide potential foraging (Gill et al. 2001; Stillman 2003) or breeding (Yasue and Dearden 2006a). Consequently, recreational activities are a central cause of population declines in many species listed as federally threatened or endangered (Czech et al.

2000). Anthropogenic disturbance can influence the habitat selection process in a number of ways, including altering the availability of habitat for individuals to choose from, influencing behavioral decision-rules animals' use during habitat selection, or by altering the fitness consequences of habitat selection (e.g., Robertson and Hutto 2006).

Nonetheless, anthropogenic disturbance can sometimes be a poor predictor of a given species presence and/or density (Gill et al. 2001; Yasue 2006; Finn et al. 2007). For example, some species settle in areas of high human disturbance, which is thought to be driven by prey abundance being high enough to compensate for negative impacts of human disturbance (Gill et al. 2001; Smith and Faillace 2006; Finn et al. 2007).

Other factors thought to alter habitat selection include food, habitat physiognomy, and predators. Food availability is an important determinant for patterns of selection and species occurrences in natural communities (Frederick et al. 1996; Granadeiro et al. 2004) due to energy requirements associated with both reproduction and survival (Schekkerman and Visser 2001). Not only does food availability have the potential to influence the spacing of individuals across the landscape (Goss-Custard 1984) , but variation in prey availability may influence the abundance of individuals at a more localized level (Evans and Dugan 1984).

Habitat physiognomy or the purely physical features of the nest-site (e.g., canopy cover, tree height, etc.) are an additional potential determinate of breeding success for most bird species (Dunning et al. 1992; Block and Brennan 1993). In particular, physical features at the nest-site may have direct consequences by affecting the probability of nest predation (Steele 1993; Budnik et al. 2002) or through providing an advantageous microclimate. Because different predators use different search tactics, physical features of the nest-site and the benefits provided likely depend upon the local predator community (Martin 1987; Soderstrom et al. 1998).

For avian species, predation is typically considered as a primary cause of failure (Ricklefs 1969; Chalfoun et al. 2002). High predation rates have been linked to the local abundance of predator species (Potts 1980; Angelstam 1986) and to high conspecific nest density (Page et al. 1983). Additionally, the influence of predator communities and abundance has the ability to influence prey use within a given habitat (Martin 1987). However, in efforts to understand the role of predation, many researchers focus on only physical habitat features associated with successful reproduction (e.g. Martin 1998; Powell and Collier 2000; Hood 2006) without knowledge of specific causes for failure. To predict patterns of predation and assess their effects on communities, it is crucial to link observed patterns of nest predation with identification of the most important nest predator species (Soderstrom et al. 1998; Chalfoun and Martin 2009). Knowledge of which predators our causing nest predation and their related foraging strategies within the environment is limited (Ricklefs 1989), largely because predation is typically impossible to measure in most systems in a meaningful way. Through the use of cameras at nests, researchers are making strides in understanding the role of predators (e.g., Bolton et al. 2007). However, the use of cameras is not always feasible, usage may impact nest survival indirectly, and sample size is often limited.

There is a need to incorporate multiple predictors related to habitat use and selection, such as the impacts of human disturbance, prey availability, and potential predation in addition to the physical features associated with the habitat (Gill et al. 2001; Stillman and Goss-Custard 2002; Yasue 2005). Such integration would allow for a more robust and accurate assessment of human disturbance and other ecological factors that may impact species-habitat relationships (Frid and Dill 2002; Yasue 2005).

Shorebirds breeding on coastal habitats provide an excellent system to address multiple hypotheses of nest-site selection. Coastal beach habitats, such as the Florida gulf coast, are rapidly declining due to habitat alteration, recreational use, and development (Chase and Gore 1989; Burger 2000; Lafferty 2001a; Lafferty 2001b). With direct pressures related to human disturbance these beaches provides a unique setting for testing the relative role of human disturbance. Moreover, with the presence of a sand dominated environment, the Florida gulf beaches provide a rare opportunity for testing multiple hypotheses through the use of tracking human and predator activity in the sand that surround shorebird nests.

I investigated alternative hypotheses for nest-site selection and subsequent reproductive success in the Snowy Plover (*Charadrius alexandrines),* a small shorebird that in Florida, nests primarily on non-developed barrier island beaches located along the Gulf Coast. The Florida plover population is listed as state threatened, as Endangered by the Florida Committee on Rare and Endangered Plants and Animals (Gore 1996), and recent surveys have documented low state-wide population estimates (n=222; Himes et al. 2007). For Snowy Plover nest-site selection and the consequent nest survival I contrasted four *a priori* hypotheses: 1) nest-site selection and survival are determined by predator activity, 2) nest-site selection and survival are determined by human activity, 3) nest-site selection and survival are determined by prey availability, and 4) nest-site selection and survival are determined by physical features of the habitat. Because habitat selection is thought to be adaptive (Clark and Shutler 1999), I predicted for both nest-site selection and nest survival in order of expected influence that (1) predator activity would have a negative influence, (2) human activity would have a negative influence, (3) prey availability would have a positive influence, and (4) physical features would have mixed and minor influences (e.g., features that provided camouflage would have a positive influence and those that conceal visibility of potential predators would have a negative influence).

Methods

Study Area

I collected data at seven sites located contiguously in Franklin, Gulf and Bay Counties, in the panhandle of Florida, comprising 67.0 km of beach habitat (Fig 2-1.). Sites included were Shell Island (5.2 km; St. Andrews State Park, 7.3 km; Tyndall Air Force Base [TAFB]), Crooked Island East, West, & Buck Beach (23.7 km; TAFB), Windmark Beach (5.2 km; St. Joe Company), St. Joseph's State Park (13 km), and St. Vincent National Wildlife Refuge (12.6 km). All sites are barrier Islands located along the Gulf Coast, except Windmark Beach and Buck Beach, which are mainland beaches. Most of my sites were on public land, with the exception of Windmark Beach and portions of Crooked Island East. Collectively these seven sites represent the largest intact portion of coastal beach habitat in Florida and the Florida Snowy Plover population (41%; Himes et al. 2007).

Nest Monitoring

I conducted nesting surveys every 5-7 days between February and August of 2008 and 2009, and I searched for nests systematically in all suitable breeding habitats at each site. With an assistant, I conducted all nest searching using a leapfrog method, with one person walking the nesting habitat and a second person using an all terrain vehicle (ATV) on the shoreline (Himes et al. 2007; Lauten et al. 2007)). Once Snowy Plovers were located, I determined if they were exhibiting breeding behavior. For nesting pairs (birds actively defending scrapes with eggs), I watched from a distance for them to return to their nest or I located the nest by following Snowy Plover tracks back to nests. For territorial pairs, (birds defending an area, but without nests containing eggs), I searched for nest scrapes and documented them for future investigations.

After nests were located, I recorded their position with a global positioning unit. If nests were located with a full clutch, I used egg floatation to detect embryo mortality and to estimate hatch dates (see Hood 2006 for age estimates*)*. For this study, I assumed an estimated egg-laying length of 4 days and incubation length of 26 days, which is normal for Snowy Plovers nesting in Florida (Chase and Gore 1989). Snowy Plovers do not begin incubating until the third egg in the clutch is laid (Page et al. 2009). Therefore, estimating hatch-date via floatation was only possible with full clutches. For incomplete clutches I estimated hatch-day by adding potential lay-days. I monitored nests every 5-7 days until cessation (i.e., eggs hatch or fail). I also visited all nests on the estimated hatch day and confirmed nests to have hatched if young were located in or near the nest site. If eggs disappeared too early to have hatched and no physical evidence (i.e., trampling, inundation, etc.) was present, I considered the nest to be depredated and looked for predator tracks at the nest site and/or egg shell evidence (Table 2-1; see Mabee 1997).

I incorporated all nests located during either breeding season in analyses, including re-nesting efforts. Snowy Plovers follow a serial polygamous mating system (Page et al. 2009). Typically, after a successful hatch, females abandon the brood and locate a new mate (Warriner et al. 1986; Paton 1995; Fraga and Amat 1996). Males after successfully fledging or losing a brood will locate a new mate (Page et al. 2009). As a result, between nesting events within a breeding season, nests are rarely between the same two individuals.

Available Habitat

To sample habitat availability I used a stratified random sampling method throughout each site. I generated random points with ArcGIS 9.2 by creating polygons of potential nesting habitat based on aerial photographs and personal knowledge of the area. I identified potential nesting habitat as the sandy beach habitat located between the shoreline and tree-line or dense vegetation, incorporating much of the sand dunes (see Himes et al. 2007). Within potential nesting habitat, I overlaid a grid system (100 m x 100 m) and ran a random point generator (Hawth's tools extension for ArcGIS) to select points within each grid. I collected habitat data at one random point for each nest located.

Explanatory Variables

I analyzed four groups of explanatory variables that might influence selection and survival during the nesting stage: physical features, human activity, prey availability, and predator activity. To do so, I collected measurements at both nest and random point locations using three spatial scales: nest-site (1 m radius), nest-territory (100 m radius), and landscape scale (500 m radius).

In previous studies on Snowy Plovers, various habitat physical features have been found to influence both selection and survival at local scales (e.g., surrounding nest sites). In particular, plover nest survival is thought to depend upon the ability to detect approaching predators (Powell 2001; Hood 2006). Consequently, I predicted a negative effect of increased vegetative cover and with proximity to dunes. I also predicted shell and organic debris in and around the nest to positively influence nest survival by providing camouflage (while still allowing visibility of approaching predators). To test these predictions, I visually quantified the percent ground cover of vegetation, bare sand, and debris at the nest-site scale within a 1 m radius. At the nest-territory scale I used a distance to object design (Williams et al. 2002), measuring the distance to vegetation, primary dune, dune height, and the distance to nearest conspicuous debris.

To test for the influence of human activity I collected data at both the nest-territory and landscape scales. Because studies have shown reproductive performance to increase with protection of habitat from human disturbance (Lafferty et al. 2006), I predicted a positive influence to nest selection and nest survival with the use of symbolic fencing and with increased distance from beach access points. Symbolic fencing is composed of signs and ropes and is often used by managers to protect nesting areas from human disturbance (see Lafferty 2001a). Although not legally enforced in many areas in Florida (Himes et al. 2007) it is considered symbolic through encouraging people to stay out of nesting areas. Within the nest-territory I documented the presence/absence of beach access points, distance to nearest human foot print, and presence/absence of symbolic fencing within a 100 m radius. At the landscape scale, I systematically sampled human activity, predicting nest-site selection and survival to decrease as human density increased. To investigate the spatial variation in human disturbance potentially affecting nest-site selection and nest success, I quantified human density with beach foot traffic. I set up strip transects by raking 50 m long x 2 m wide sand transects running perpendicular from the shoreline to the primary dune line. Transects were set-up over the weekend to capture maximum beach activity levels. To investigate temporal variation, I conducted sampling twice during both breeding seasons. The first sampling occasion took place during the months of March and April and the second sampling took place during June and July.

To test for the influence of prey availability, I collected data at both the nest-territory and landscape scales. I categorized foraging habitat into three foraging types (ephemeral pools, bay flats, and gulf front; Table 2-2). Broods with easy access to foraging locations tend to have higher survival rates (Loegering and Fraser 1995); therefore, I predicted plovers would select nest sites in close proximity to high prey foraging locations. Adults nesting closer to foraging habitat likely benefit through nest attentiveness (Yasue and Dearden 2006b); therefore, I predicted prey availability to positively influence nest survival. To test these predictions, within the nest-territory I measured the distance from the nest to the nearest foraging habitat and identified the type of the nearest foraging habitat within a 100 m radius. At the landscape scale, I used a 500 m x 500 m grid and categorized each grid by the presence of foraging habitat types. I classified grids as ephemeral or bay flats if one of these habitat types were present. If neither of these two foraging habitats were present, I classified the grid as shoreline foraging habitat.

To test the influence of predator activity, I collected data at both the nest-territory and landscape scales. Avian predators, such as fish crows (*Corvus ossifragus*) are often associated with forest patches. The forest patches located at these sites are composed primarily of slash pine (*Pinus elliottii*). Therefore, I recorded the presence/absence of the sand pine forest edge within a 100 m radius. Previous studies have suggested that ghost crabs depredate plover nests (Watts and Bradshaw 1995; Himes et al. 2007). Thus, I measured to the nearest ghost crab burrow from the nest. Beyond the perceived predator threat, I was interested in how the change in predator activity levels impacted selection and survival based on predictions that selection and survival would decrease in response to increased predator densities. Therefore, at the landscape scale I systematically sampled predator activity through tracking. Tracking animals by following footprints in substrates such as sand is probably the oldest known and most efficient method of identifying mammal presence in an area (Bider 1968; Silveira et al. 2003). I set up strip transects by raking 50 m long x 2 m wide sand transects running perpendicular from the shoreline to the primary dune line. I sampled transects once after a two-day period. Per transect, I counted the number of ghost crab burrows present, the number of observed predator tracks to account for other predator species (e.g., coyotes, raccoons, etc.), and the number of avian predators observed in the area (e.g., fish crows). To investigate potential temporal variation, I sampled transects twice during both breeding seasons. The first sampling occasion took place during the months of March and April and the second sampling took place during June and July.

Statistical Analysis

Nest-Site Selection

To model nest-site selection, I used logistic regression to model the probability of nest-site selection as a function of the variables collected at all spatial scales that represented the *a priori* hypotheses. The response variable was whether habitat was used (i.e. with the presence of a nest) or available. I used the Generalized Linear

Model (GLM) procedure within R (2008) to estimate regression coefficients with the logistic models.

Nest Survival

To estimate nest survival, I used the logistic-exposure method which accounts for variation in exposure days among nest visits (Shaffer 2004). I used the GLM procedure within R (2008) to estimate regression coefficients in the logistic-exposure models. Using this method, I estimated daily nest survival rates from the resulting logistic function (Shaffer 2004). I used the effective sample size (*n*; Rotella et al. 2004) when analyzing model fit (i.e., *n* = total number of days that nests were known to survive + the total number of intervals in which a failure occurred). The response variable was whether or not the nest survived the interval between visits.

Model Selection

Because I had many predictor variables (Table 2-3), I used a Spearman's non-parametric correlation matrix to check for potential multi-collinearity (Appendices A & B). After confirming that no variables were strongly correlated ($r > |0.6|$), I selected the best approximating model(s) using Akaike's Information Criterion for small sample sizes (AIC_C) (Burnham and Anderson 2002; Anderson 2008).

I first developed the most parsimonious model for explaining variation in nest-site selection or nest survival for each *a priori* hypothesis (prey availability, predator activity, human activity, and physical features) by using a manual forward model selection approach using AICc. The most parsimonious model for each hypothesis was then contrasted using AICc alongside a null (intercept-only) model. Because these hypotheses are not mutually exclusive, I also explored the potential for these hypotheses to be operating in concert by considering additive effects of these hypotheses.

Results

Nest-Site Selection

During the 2008-9 breeding seasons, I located 473 nests (2008: 190; 2009: 283). Overall, there was some evidence for each hypothesis in the predicted direction; with models representing each hypothesis fitting the data better than an-intercept only model (Table 2-4). However, the only strongly supported model contained at least one explanatory variable from each of the *a priori* hypotheses. During both years, plovers selected habitat based on physical features, human activity, predator activity, and prey availability. Specifically, plovers selected locations near conspicuous beach debris, near ephemeral pools, away from ghost crab burrows, away from forest patches, and with the presence of symbolic fencing (Table 2-4 and Fig. 2-2a-e).

Nest Survival

I monitored the fate of 473 nests during the 2008-9 breeding seasons, resulting in an effective sample size of 6728 (see *Statistical Analysis*). The mean interval length between nest visits for both years was 6 days. Pooled across both seasons, I observed an apparent nest survival rate of 0.437.

Approximately 88% of all unsuccessful nests during both seasons failed due to known depredation. In 2008 and 2009, I identified ghost crabs as the most common predator of eggs (Table 2-5.), accounting for 64% of identified depredation events based on tracks at the nest site. Coyote were the second most identified predator, whereas fish crows only represented 2% of depredation events. Based on predator sampling pooled across both seasons, I identified 6266 individual tracks. Of the total count, 92% represented ghost crab burrows (n=5783). In comparison, only 5.2% of tracks were from coyotes (n=324).

There was some evidence for each hypothesis; with models representing each *a priori* hypothesis fitting the data better than an-intercept only model (Table 2-6). However, there were two competing models with similar AICc values. Explanatory variables from three of the *a priori* hypotheses combined produced the most parsimonious model and the second best model contained predictors from each of the four hypotheses. Based on these two additive models, plovers were more likely to hatch a nest in areas further from ghost crab burrows, with the presence of symbolic fencing, in locations further from foraging habitats, and when located further from conspicuous beach debris (Fig. 2-3a-d). Human and predator activity were in the predicted direction, however prey availability and physical features were the opposite of what I predicted and what was selected for in nest-site selection.

Discussion

Few habitat studies have been able to confront multiple ecological hypotheses for habitat selection, nor the fitness consequences of such decisions (Jones 2001). My results provide a unique demonstration of how multiple selective forces influence nest-site selection and reproductive output. Additionally, through the use of tracking I was able to link predator counts with observed patterns of nest predation and with the identification of the most important nest predator species in this region. Nest-site selection and nest survival patterns revealed in this study indicate an influence by a combination of environmental influences working in concert. Nest-site selection and the consequent survival were influenced by human and predator activity, prey availability in addition to physical features surrounding the nest-site.

Human Activity

Along the gulf coast of Florida, the presence of human activity on beaches has the ability to reduce habitat quality (i.e., in terms of survival). Plovers were four times more likely to nest in areas protected from human activity. Previous studies have also shown benefits from restricting human disturbance (Lafferty et al. 2006; Lauten et al. 2007). Additionally, species from various taxonomic groups shift habitat use in response to human disturbance including dolphin (Allen and Read 2000), geese (Gill et al. 1996), and bear (Mace et al. 1996). There are many potential benefits associated with protection from human disturbance. However, on coastal beaches without protection, human activity can lead to direct trampling of nests (Yasue and Dearden 2006a; Page et al. 2009). Human activity may also indirectly impact success through the flushing of individuals from nests (Frid and Dill 2002; Yasue and Dearden 2006a), leaving eggs exposed to predators in the process (Page et al. 2009) or exposed to the sun resulting in embryo mortality (Webb 1987).

Although plover nests were twice as likely to hatch with the presence of symbolic fencing, there were very few nests impacted by direct pressures from human disturbance (n = 15 (3%), abandoned; n = 0, trampled). In fact, the primary cause for failure in areas not protected against disturbance was depredation and the main source documented was from ghost crabs. The occurrence of crab depredation in locations not protected from disturbance suggests potential indirect mechanisms by which ghost crabs respond to cues related to disturbance activity at the nest itself. Frid and Dill (2002) have hypothesized that increases in indirect predation rates in association with human disturbance are related to predation risks as a result of disturbance stimuli.

However, the resulting predation rates may be linked to the particular behavior of existing predators and how they search for prey (Sodersrom et al. 1998).

Predator Activity

The ghost crab is a unique predator within the Snowy Plover's geographic range and appears to be isolated to the Florida population. In addition to Snowy Plovers, I documented Least Tern (*Sternula antillarum)* and Wilson's Plover (*Charadrius wilsonia*) nests depredated by ghost crabs. This is the first study that I know of to quantify the relationship between ghost crabs and plovers in Florida, although crabs are frequently documented as predating upon lizards and sea turtle hatchlings on the same beach habitats (Wolcott 1978; Strachan et al. 1999). The influence of ghost crabs on nest-site selection is likely due to a perceived predation risk to both adult and nest survival. In addition to ghost crabs depredating eggs and chicks, adult plovers are often observed with leg or body wounds from ghost crabs (pers. Obs.). The impacts from crabs on adult survival and population dynamics are currently unknown.

Nests that were closer to burrows were less likely to survive. Comparably, previous studies have documented higher hatch rates in areas of low crab burrow densities (Yasue and Dearden 2006a). Interestingly however, no abandoned nests (n = 15) in my study were depredated by crabs, therefore, predation likely occurs because ghost crab's respond to visual stimuli associated with the nest. In addition, ghost crab predation might occur indirectly. When plovers are approached by people they flush from the nest and conduct distractive displays (Yasue and Dearden 2006a; Baudains and Lloyd 2007; Weston and Elgar 2007). This behavior may impact nest survival in two ways. First, the plover leaves eggs exposed to predators upon leaving the nest. Second and possibly more important in this system, conspicuous activity associated with anti-predator displays by plovers may increase predation risk. The visual stimuli associated with such displays may encourage predation from ghost crabs. Unlike many crab species, ghost crabs are not scavengers, but active predators (Wolcott 2009) and are among the fastest terrestrial invertebrates (Full and Weinstein 1992). During a study on ghost crab diet, Wolcott (1978) found ghost crabs to rely on live beach macrofauna for 90% of its diet. Ghost crabs are largely nocturnal, but flexible in their behavior and can forage by day (Wolcott 2009). During the day crabs remain closer to their burrows, cleaning and foraging around it (Wolcott 1978). However, the ability for diurnal ghost crab activity is dependent upon crab size. Large crabs are able to tolerate higher temperatures and can stray further from the water and their burrows (Wolcott 2009). Additionally, Wolcott and Wolcott (1999) suggest that the relationship between plovers and crabs may be dependent on climate and latitude. Ghost crabs increase in size and abundance from their northern to southern limits along the Atlantic Coast (U.S. Fish and Wildlife Service 1996). Thus, because of ghost crab behavior and size in Florida, plover anti-predator displays may be maladaptive at this location.

Interestingly, nest survival was lowest for nests located in close proximity to foraging habitats. The additive influence of distance to the nearest water body may exacerbate the influence of human disturbance stimuli and the consequent indirect predation. I collected information on foraging habitats to test for the influence of prey availability with specific predictions related to increased nest attentiveness. However, the relationship between the distances from nest to water is likely an influence of beach width. Beach-goers typically walk the water’s edge, resulting in greater frequency and intensity of disturbance with closer proximity to foraging habitat from the nest. The resulting disturbance is likely too great to provide an observable benefit to nest survival through adult attentiveness. Increased predation likely results from the human disturbance stimuli related to distance to foraging habitat.

The decline in the probability of nest-site selection in relationship to the presence of forest patches is likely related to a perceived predation risk to both adult and nest survival. The presence of forest patches did not result in an impediment to hatching a nest. However, the probability of nest placement in the presence of forest patch was less than 10 %, therefore, the potential to observe a fitness consequence in response to the presence of a forest patch in study was limited. Yasue and Dearden (2006a) observed Malaysian plover (*Charadrius peronii*) nest settlement patterns to be influenced by the percent cover of tall trees backing the beach. Foraging shorebirds wintering in British Columbia also preferentially select areas further from forest cover (Yasue 2006). The selection pattern in response to forest patches is thought to occur because trees provide cover from which avian predators launch attacks (Lazarus and Symonds 1992). In this study both predictors in relation to predator activity that influence nest selection probability were related to perceived predator risk rather than with the change in predator densities across the landscape. However, the type of predators observed and abundance of each type through tracking matched the recorded nest predation events trough tracking evidence at individual nests.

Physical Features

Researchers have long hypothesized the placement of nests adjacent to debris to provide an advantage in nest survival (Graul 1975). Yet the debris in question is usually too small to provide any protective advantage from weather (Purdue 1976). Therefore, the presence of debris is thought to provide visual obstruction from potential predators

(Powell 2001). Effects on nest survival, however, are equivocal. Many studies have identified an increase in nest survival with the presence of debris (Hood 2006; Grover and Knoff 1982), yet others have observed the opposite pattern (Cohen et al. 2008; Powell 2001). Hood (2006) speculated this discrepancy was due to the amount of debris present in the landscape, suggesting that in areas with less debris, predators may actually be attracted to nests because they are located next to debris. Within my study sites, however, the availability of debris was not limiting. Therefore, the inconsistency in nest survival in relation to beach debris is likely a response from localized predator communities. Because different predators use different search tactics, predation rates and habitat influences likely differ among locations (Martin 1987; Soderstrom et al. 1998). Powell (2001) suggested that corvids follow the debris line in search of nests in coastal California, resulting in increased predation with the presence of debris. Hood (2006), in contrast, reported coyotes to be the major cause for depredation in Texas and observed an increase in survival with debris. In my study ghost crabs were the major cause for depredation. Because ghost crabs respond to movement, debris likely provides no nesting benefit to plovers nesting in Florida. Additionally, ghost crabs are sensitive to high temperatures (Strachan et al. 1999; Wolcott 2009) and consequently, often build burrows under or adjacent to beach debris, which provides shade.

Nesting adjacent to beach debris appears to be maladaptive in relation to nest survival throughout much of the Snowy Plovers geographic range. However, animals seeking habitat may be attracted to cues for several different reasons. In addition to responding to cues that directly impact fitness, cues may simply be correlated with more relevant habitat features, such as potential nest sites (Stamps and Krishnan 2005; Chalfoun and Martin 2009). The latter suggests that cues might be indirectly related to habitat quality or such cues merely improve the ability for an individual to detect potential habitat (Stamps and Krishnan 2005). Therefore the presence of debris may be indirectly related to greater habitat quality. Additionally, with subsequent work with brood survival I documented an increase in daily survival with a greater percentage of debris around the immediate nest site (Chapter 3). Thus, birds might also be responding to cues which provide benefits post-hatch.

Prey Availability

Across all sites, plovers were more likely to nest in close proximity to ephemeral pools. Additionally, ephemeral pools provide a greater abundance of prey items when compared to the other two foraging habitat types (Chapter 3). By nesting in close proximity to high quality foraging habitat and limiting the occurrence of a potentially hazardous journey may increase overall reproductive success (Loegering and Fraser 1995; Kosztolanyi et al. 2007). Therefore, plovers are likely selecting habitat in close proximity to ephemeral pools to provide easy access to foraging habitat for use beyond the nesting stage. The selection of landscapes that provide resources for more than one requirement is not unprecedented (see Dunning et al. 1992 on complementary landscapes). For instance, many avian species require one habitat for foraging and an entirely separate habitat for roosting (Petit 1989; Dias et al. 2006). For a species with precocial young, the requirements between breeding stages (where one stage is sessile and the other mobile) are likely distinct. Consequently, the selection of nesting habitat likely takes into account requirements for both stages because they are both necessary for survival. However, nests closer to foraging habitat were less likely to survive to hatching.

Conclusions

It is inevitable that human populations will increase and as populations increase, the occurrence of habitat alteration and direct impacts will follow. The sites sampled during this study represent the largest intact portion of the Snowy Plover nesting sites remaining in Florida (Himes et al. 2007). However, even at these lower spectrums of human disturbance levels, plovers benefited by the protection from human activity (i.e., use of symbolic fencing). These sites remain intact because they are primarily publicly owned and protected from direct anthropogenic habitat alteration (i.e., development, etc). Although they remain public lands, they are not immune to spillover from human disturbance from neighboring sites which participate in development. As anthropogenic pressures increase, so will the need to protect beach nesting species from the impacts related to disturbance.

The primary source of nest depredation observed in this study is vastly different from the predator pressure observed in other geographic regions. In many regions, exclosures are used as a means of protecting nests from predation and are primarily useful in preventing mammals and corvids from accessing shorebird eggs (Lauten et al. 2007). However, such management would likely have no influence in protecting nests from predation in the Florida population. Management efforts geared toward the conservation of plover populations may therefore need to be customized to the predators primarily responsible for local nest mortality based on geographic location.

In addition to the influences of predator activity, I explored the influences of physical features, human activity, and prey availability on nest-site selection and addressed whether these influences were or were not adaptive (i.e., in terms of survival; see Table 2-7). Using a species that is well studied throughout most of its range, for which there is conflicting reported habitat requirements and variable pressures, this study quantitatively demonstrated the importance of testing multiple ecological hypotheses and the corresponding influence of multiple predictors. Collectively, consideration of multiple predictors in habitat management, which is relevant to wildlife in general, will benefit the conservation of rare and declining species.

Table 2-1. Predation descriptions based on predator types present on the beaches in Florida Panhandle, 2008, 2009.

Predator	Distinguishing features
Ghost Crab	Ghost crab tracks present at the nest coming directly from burrow to nest. Egg shell fragments often remain with jagged edges and were typically strung out between the nest and burrow. Nests categorized as a ghost crab predation if obvious tracks were present and/or the presence of egg fragments, but never with only the presence of egg fragments at the nest and no obvious tracks.
Coyote	Nests were categorized as depredated by coyotes if coyote tracks were present at the nest itself and not in the surrounding area.
Fish Crow	Unlike the other predator types, crow tracks aren't observed throughout the habitat. They typically land a meter from a nest and walk the rest of the way to the nest leaving a row of tracks in the process. Eggs are typically gone, likely swallowed whole. A few have been observed intact with holes from the bill.
Raccoon	Nests were categorized as depredated by raccoon if raccoon tracks were present at the nest itself and not in the surrounding area. Raccoons typically work the area looking for the eggs, thus the nest is plastered with tracks and the evidence is unmistakable
Unknown	If no obvious tracks were present at the nest, even if crab burrows were nearby and light crabs tracks were observed at or near the nest, and the nest disappeared too early to have hatched, nests were categorized as depredated by an unknown predator. Additionally, if more than one obvious predator tracks were observed at the nest it was considered as unknown.

Table 2-2. Foraging habitat types of the Gulf Coast of Florida.

Habitat Type*	Distinguishing features
Ephemeral pool	Low energy, standing water pool with surrounding moist sand. Typically with sparse to medium vegetation, but backed by dunes with denser vegetation. Standing water derives from either high tide or storm activity due to the presence of low dips located between the shoreline and dune line.
Bay tidal flat	Mud flats submerged only at high tide. Are generally only reached by waves of low amplitude, resulting in moist sand. Typically sparsely vegetation, flat, and exposed. Some salt-tolerant plants (mostly *Salicornia* and *Spartina*).
Shoreline	High to medium energy wave dominated. Moist sand limited to the swash zone, where waves are projected up the beach slope. Typically with standing wrack (largely composed of dead marsh grass) and sparse vegetation, but backed by dunes with dense vegetation. Can be located on either the gulf or bay sides. Foraging restricted to between the shoreline and the foredunes.

* Habitat type definitions modified from Davis and Fitzgerald (2004)

Table 2-3. Explanatory variables considered in the analysis of Snowy Plover Nest-site selection and survival, Gulf Coast of Florida, 2008–2009

Variable	Description
Physical Features	
Veg	Percent vegetation cover at 1 m radius
Sand	Percent sand cover at 1 m radius
Debris	Percent debris cover at 1 m radius
DistVeg	Distance to the nearest vegetation within 100 m radius
DistDune	Distance to the nearest dune within 100 m radius
DuneHgt	Height of the nearest dune
Distdebris	Distance to the nearest conspicuous debris within 100 m radius
Prey Availability	
DistWater	Distance to the nearest foraging habitat within 100 m radius
TypeForaging	Type of the nearest foraging habitat
Foraging	Presence of foraging habitat at 500 m
Predator Activity	
Forest	Distance to the nearest forest patch within 100 m radius
GhostCrab	Distance to the nearest ghost crab burrow within 100 m radius
Predator	Total count of observed predator tracks at 500 m
Human Activity	
Fencing*	Presence/absence of symbolic fencing within 100 m radius
Access	Presence/absence of beach access points within 100 m radius
DistHuman	Distance to the nearest human footprint within 100 m radius
Human	Total count of observed human tracks at 500 m

*Fencing considered present for nest-site selection models if already present prior to nest settlement and considered present for nest survival models if fencing materials were present already or if they were erected after nest settlement.

Table 2-4. Nest-Site Selection models based on *a priori* hypotheses for Snowy Plovers (n= 946) on the Gulf Coast of Florida, 2008, 2009. Models are ranked based on Akaike's Information Criterion for small samples (AICc), AICc is based on -2LL, which is the value of the maximized log-likelihood function of the model parameters given the data set, the number of parameters (K), and Δ AICc is the AICc differences relative to the smallest AICc in the model set.

Hypothesis*	K	AICc	-2LL
Physical Features			
DistDebris	2	929.07	-925.06
Prey Availability			
TypeForaging	3	1119.39	-1113.37
Predator Activity			
GhostCrab+Forest	3	1000.07	-1001.04
Human Activity			
Fencing	2	1032.78	-1028.76
Intercept Only	1	1229.93	-1227.93
Best Additive Model			
DistDebris+TypeForaging+GhostCrab+Forest+Fencing	7	599.67	-585.54

*DistDebris= distance (m) to the nearest conspicuous debris, TypeForaging= categorical type of foraging habitat, Ghostcrab= distance (m) to the nearest burrow, Forest= presence/absence of Forest patch within 100 m of nest, Fencing= the presence/absence of symbolic fencing around nests.

**Best Additive Models include those < 2 ΔAICc from the best model.

Table 2-5. Number of nest predation events at Snowy Plover nests based on tracking evidence at the nest on the Florida Gulf Coast, 2008, 2009

Predator	2008	2009	Total
Coyote	14	35	49
Fish Crow	2	2	4
Ghost Crab	37	68	105
Raccoon	1	4	5
Unknown*	29	38	67
	83	147	230

*Unknown= nests that were depredated, but no tracking evidence was present at the nest

Table 2-6. Nest Survival models based on a priori hypotheses for Snowy Plovers (n= 473) on the Gulf Coast of Florida, 2008, 2009. Models are ranked based on Akaike's Information Criterion for small samples (AICc), AICc is based on -2LL, which is the value of the maximized log-likelihood function of the model parameters given the data set, the number of parameters (K), and Δ AICc is the AICc differences relative to the smallest AICc in the model set.

Hypothesis*		K	AICc	-2LL
Physical Features				
	DistDebris	2	1258.78	-1254.78
Prey Availability				
	DistWater	2	1254.07	-1250.07
Predator Activity				
	GhostCrab	2	1212.36	-1208.36
Human Activity				
	Fencing	2	1233.16	-1229.16
Intercept Only		1	1261.54	-1259.54
*Best Additive Model(s)***				
	GhostCrab+DistWater+Fencing	4	1183.73	-1175.72
	Ghostcrab+Fencing+DistDebris+DistWater	5	1184.14	-1174.12

*Ghostcrab= natural log of distance (m) to the nearest burrow. Debris=natural log of distance (m) to the nearest conspicuous debris. Other variables were not transformed: Distwater= distance (m) to nearest foraging area, Fencing= the presence/absence of symbolic fencing around nests.

**Best Additive Models include those < 2 ΔAICc from the best model.

Table 2-7. Synthesis of influences: was nest-site selection adaptive or not?

Hypothesis	Predictions*	Nest-site Selection	Nest Survival
Human Activity	-	-	-
Predator Activity	-	-	-
Prey Availability	+	+	-
Physical Features	±	+	-

*Predictions based on both nest-site selection and survival

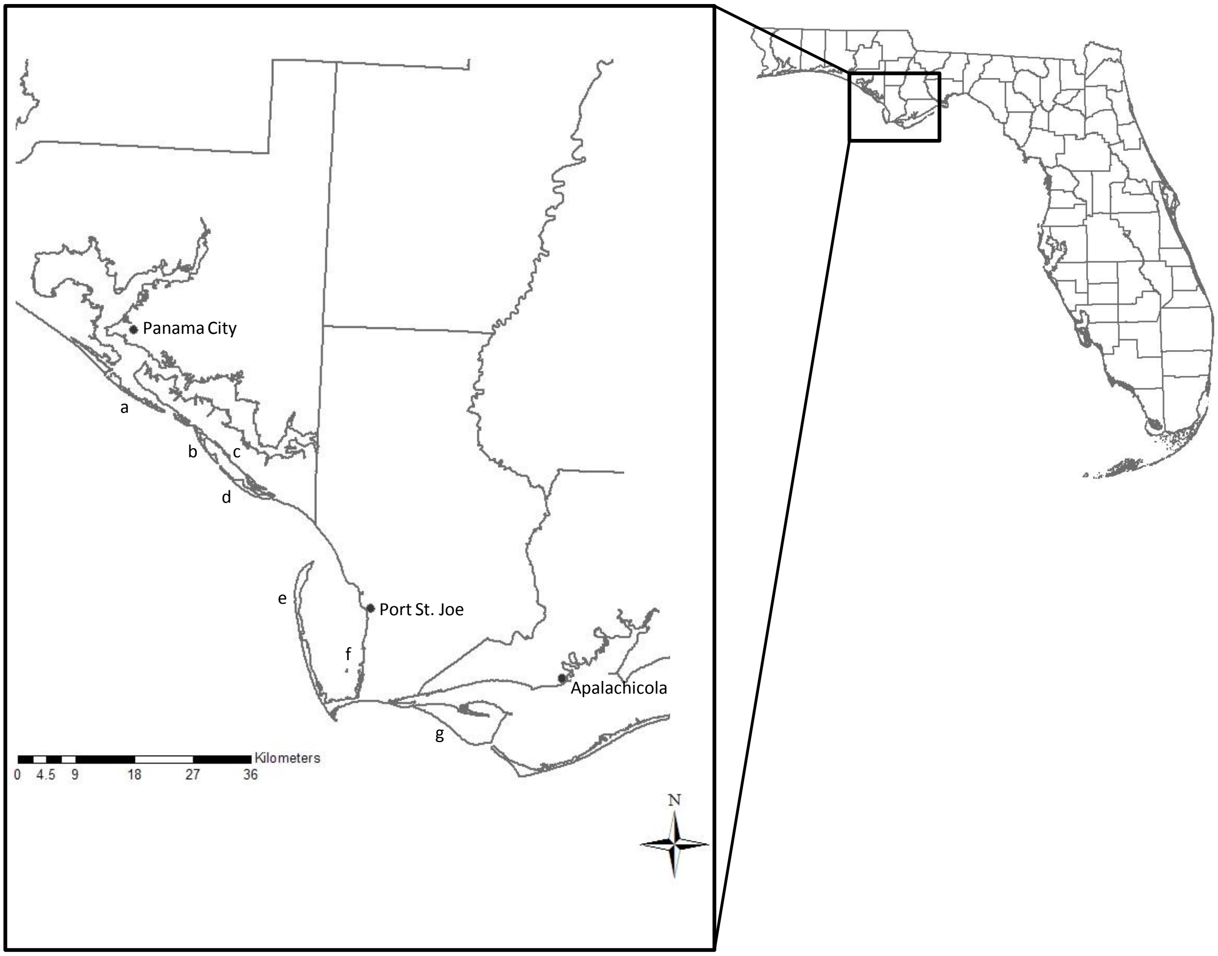

Figure 2-1. Map of Snowy Plover study sites in the Florida panhandle, USA, 2008, 2009, a) Shell Island, b) Crooked Island West, c) Buck Beach, d) Crooked Island East, e) St. Joseph State Park, f) Windmark Beach, g) St. Vincent National Wildlife Refuge.

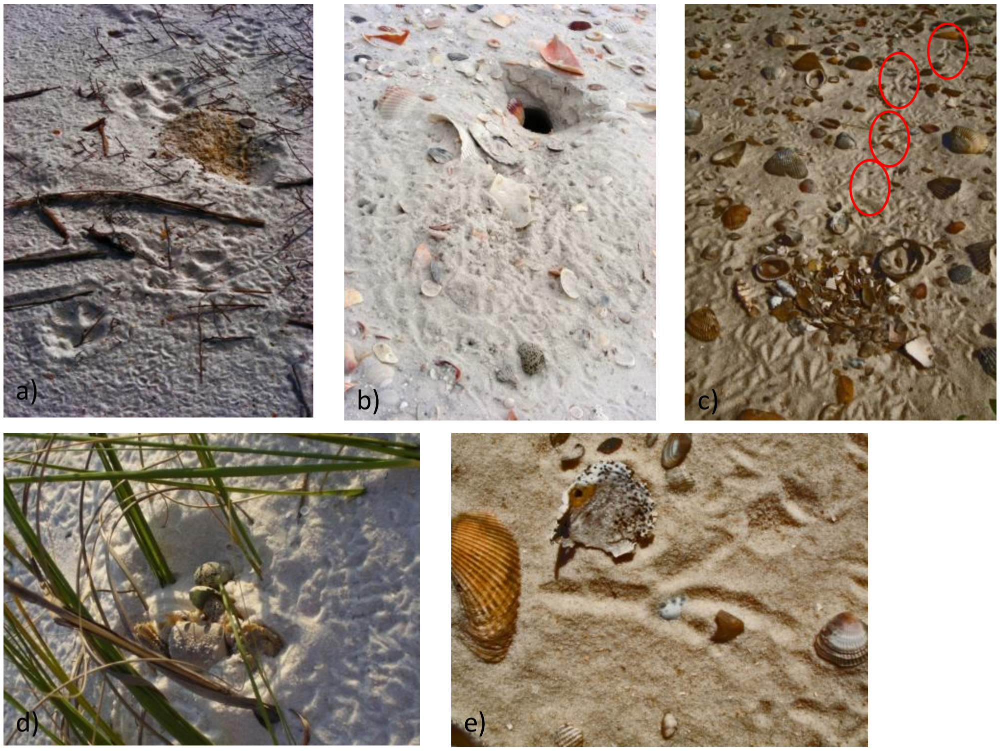

Figure 2-2. Depiction of predation events by different predator types present on the beaches in the Florida Panhandle, 2008, 2009, a) coyote tracks and spilt yolk at nest, b) ghost crab burrow, tracks, and egg drug from nest to burrow, c) crow tracks outlined with red circles leading to nest, d) ghost crab at nest depredating eggs showing body imprint left at nest, e) close up of crow tracks left at nest.

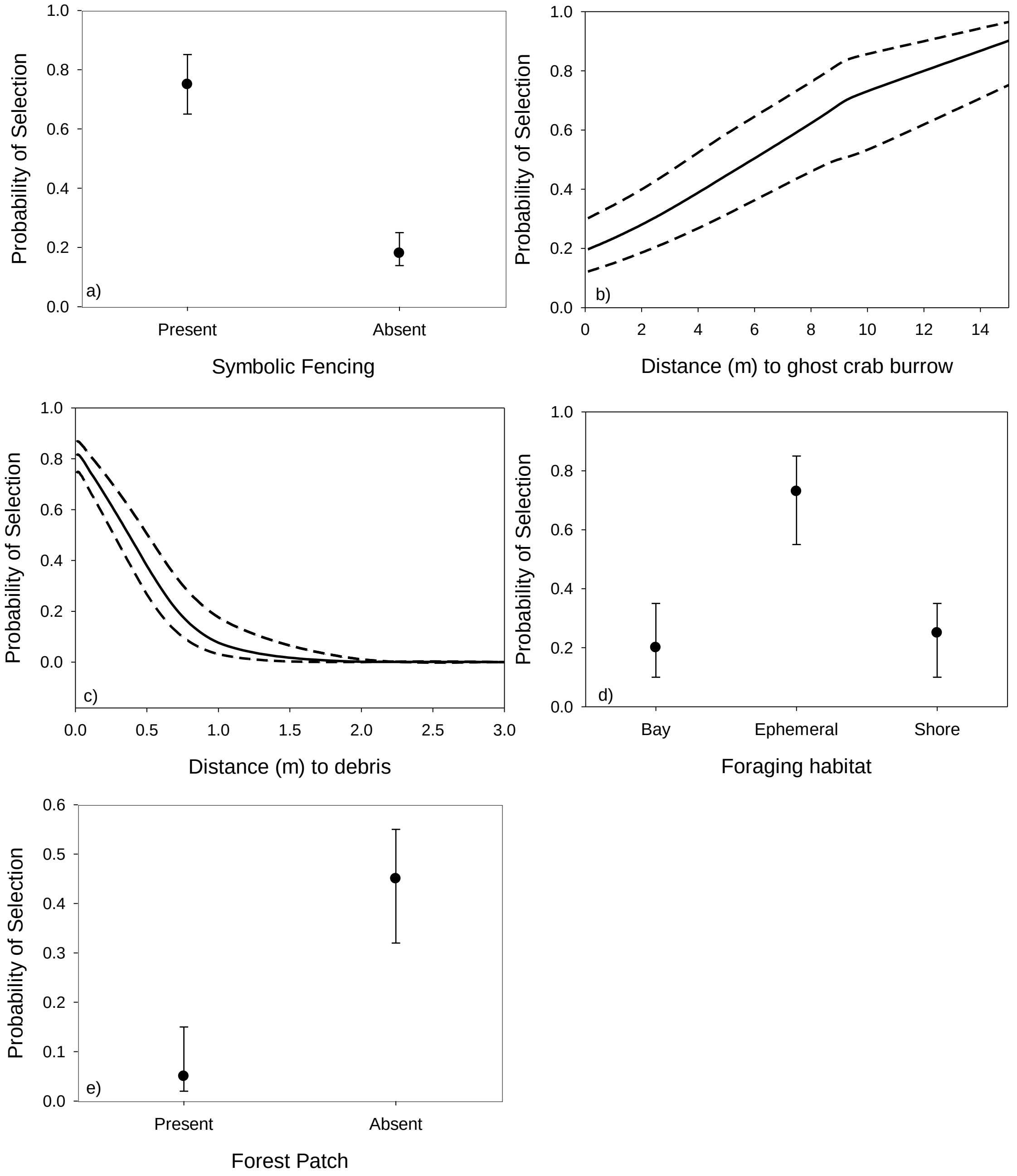

Figure 2-3. The probability of Snowy Plover Nest-Site Selection as a function of predictors from the most parsimonious model with 95% confidence limits, a) the presence of symbolic fencing within a 100m radius, b) the distance to the nearest ghost crab burrow within 100m radius, c) the distance to the nearest conspicuous debris within 100m radius, d) the nearest foraging habitat type within 100m radius, and e) the presence of forest patches within 100m radius on the Gulf coast of Florida, 2008, 2009.

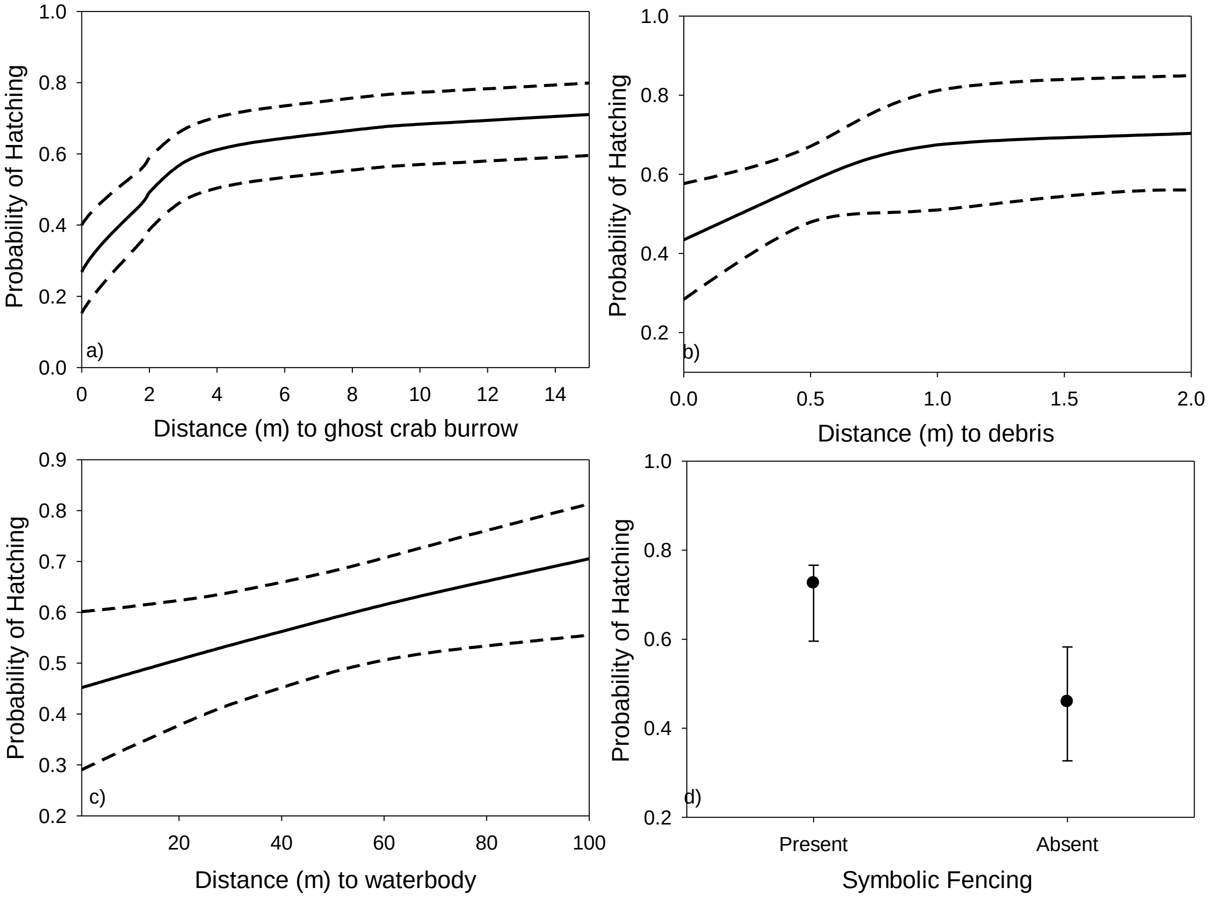

Figure 2-4. The probability of Snowy Plovers successfully hatching a nest (26 days incubation) as a function of predictors from the most parsimonious model(s) with 95% confidence limits, while holding all other values at their mean; a) the distance (m) to the nearest ghost crab burrow within 100m radius, b) the distance (m) to the nearest conspicuous debris within 100m radius, c) the distance (m) to the nearest water body, and d) the presence of symbolic fencing within a 100m radius on the Gulf coast of Florida, 2008, 2009.

CHAPTER 3
PREY AVAILABILITY AND PREDATOR ACTIVITY AS PREDICTORS OF SNOWY PLOVER BROOD-REARING SITE SELECTION AND SURVIVAL

Introduction

The selection of breeding habitat by birds may be influenced by a combination of factors, including human recreational activities, predation of young, food availability, and habitat substrate (Hoover and Brittingham 1998; Newton et al. 1998; Jones 2001; Colwell et al. 2007a). Although knowledge of such selection factors is important for species conservation, perhaps more important is an understanding of how selection factors influence survival and reproductive performance (Martin 1992; Benson et al. 2010). The selection of habitat is assumed to be adaptive, such that habitat preferences confer fitness benefits over other alternatives (Jones 2001). However, fitness consequences may become decoupled from selection factors due to anthropogenic change or alteration (Schlaepfer et al. 2002; Robertson and Hutto 2006).

Many species must find suitable habitat for multiple reproductive behaviors within a single landscape. This phenomenon is often referred to as landscape complementation (see Dunning et al. 1992). For a particular organisms resources are non-substitutable; that is, both resources are required, but for different reasons. For example, species with precocial young (e.g., waterfowl, shorebirds, etc.) must select habitats that provide adequate nesting and brood-rearing opportunities (Haig et al. 1998; Conway et al. 2005). Because the habitats used for these two distinctive stages of reproduction likely provide disparate resources, the factors influencing selection of brood-rearing habitat may be vastly different than those that influence nest-site selection. Consequently, factors effecting brood survival likely differ from those impacting nests. Estimating survival to fledging is a valuable tool in population management, but most reproductive studies with precocial species only deal with the probability of hatching eggs. Therefore, although an important component of productivity, the survival of precocial young is poorly understood.

For most species food availability is a major determinant for patterns of selection and species occurrences in natural communities (Frederick et al. 1996; Granadeiro et al. 2004) due to energy requirements associated with both reproduction and survival (Schekkerman and Visser 2001). All animals require food and most must leave offspring in order to actively search for prey in order to survive (Pyke et al.1977). Yet for precocial species, the collection of necessary food is shifted to the chick (Schekkerman and Visser 2001). Thus, precocial young must have an accessible and reliable food supply. Nonetheless, for most precocial species foraging requirements and related movement needs are largely unknown. This information gap is, in part, due to the mobility of many of these species. For example, most shorebird chicks typically leave nesting territories within hours after hatching (Page et al. 2009).

Across taxa, predation of the young is often the primary source of reproductive failure (Page et al. 1983; Angelstam 1986; Warriner et al. 1986; Martin 1992). When predation rates differ between locations, predation can influence habitat use and selection (Martin 1995; Chalfoun et al. 2002). For avian species, predation risks also vary with nest placement (e.g. ground or shrub nests, Martin 1993). Ultimately, however, the observed variation in patterns of nest predation is determined by the distribution, abundance or species composition of nest predators and their specific foraging behaviors in different locations (Martin 1987; Ricklefs 1989; Andren 1995; Chalfoun et al. 2002). Because predators likely use different search tactics (Soderstrom et al. 1998), habitat physiognomy or the purely physical features of the nest-site may have direct consequences by affecting the probability of nest predation (Steele 1993; Budnik et al. 2002)

While physical features, predators and food can be influential in offspring survival, there have been few rigorous attempts to understand the relative role of human disturbance. Alteration and loss of habitat have intensified the spatial overlap between wildlife and humans (Weston and Elgar 2007). Increases in human-wildlife contact can alter use-patterns within the landscape by excluding individuals from potential habitat (Gill et al. 2001; Stillman 2003). For example, tourism has resulted in increased recreational pressures on coastal habitats and has contributed to global declines in many coastal-dependent species, particularly shorebirds (Burger 2000; Gill et al. 2001; Lord et al. 2001; Ruhlen et al. 2003; Yasue and Dearden 2006a).

I tested for the role of prey availability, predator activity, human activity, and physical features on habitat use and survival of Snowy Plover (*Charadrius alexandrines)* broods (i.e., chicks from the same nest, dependent on parents and not capable of flight) in Florida. Snowy Plovers breed primarily on non-developed barrier islands in Florida. Snowy Plovers in Florida are listed as Threatened and as Endangered by the Florida Committee on Rare and Endangered Plants and Animals (Gore 1996), with the most recent state-wide census estimating only 222 breeding pairs (Himes et al. 2007). The plover breeding season overlaps with the coastal tourism season (Chase and Gore 1989; Lamonte et al. 2006; Himes et al. 2007), thereby exposing plovers to elevated human disturbances. Indeed, as Florida’s economy is dominated by tourism centered on coastal areas, these plovers are increasingly threatened by anthropogenic habitat change and from direct and indirect human disturbance pressure. Despite the rapidly changing habitat, no detailed or quantitative studies have been conducted on the brood rearing requirements of shorebird species nesting on Florida's beaches. Because of the ease in observing human and predator tracks in the sand, the Florida coastal beach habitat provides a unique opportunity for testing multiple hypotheses regarding brood habitat use and survival within the same study. For Snowy Plover brood-site selection and the consequent brood survival I confronted four *a priori* hypotheses: 1) nest-site selection and survival are determined by predator activity, 2) nest-site selection and survival are determined by human activity, 3) nest-site selection and survival are determined by prey availability, and 4) nest-site selection and survival are determined by physical features of the habitat. Because habitat selection is thought to be adaptive (Clark and Shutler 1999), I predicted for both brood-site selection and brood survival in order of expected influence that (1) prey availability would have a positive influence, (2) predator activity would have a negative influence, (3) human activity would have a negative influence, and (4) physical features would have a positive influences.

Methods

Study Area

I collected data at six sites located contiguously in Franklin, Gulf and Bay Counties, in the panhandle of Florida, comprising 61.8 km of beach habitat. Sites included were Shell Island (5.2 km; St. Andrews State Park, 7.3 km; Tyndall Air Force Base [TAFB]), Crooked Island East, West, & Buck Beach (23.7 km; TAFB), St. Joseph's State Park (13 km), and St. Vincent National Wildlife Refuge (12.6 km). All sites except Buck Beach are barrier Islands along the Gulf Coast. Many potential predators are present on the study area. The main predators observed at these sites in previous plover studies, include coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and ghost crabs (*Ocypode quadrata*) (Himes et al. 2007). Himes et al. (2007) also documented fish crows (Corvus ossifragus), California gulls (*Larus californicus)*, and gull-bill terns (*Gelochelidon nilotica)* impacting either nests or chicks.

Brood Monitoring

After first conducting nesting surveys, for concurrent research with nest-site selection and associated survival (Chapter 2), I conducted brood monitoring every 5-7 days between April and August of 2008 and 2009. The earliest hatch date during either season occurred on April 5th. On hatch day, I attempted to capture and band both adults and chicks. Adults were caught using a modified funnel trap and a chick coral (placed around chicks) shortly after hatching (see Gratto-Trevor 2004). I marked chicks with unique band combinations on hatch day or if they have already left the nesting area, upon the first encounter. I monitored marked adults and chicks until fledging to determine brood success. For marked individuals with recent hatches (i.e., had not fledged yet), I watched for either presence of chicks or for family behavior (i.e., actively defending territory, flying around, and/or vocalization). If marked adults were observed initiating a new territory, nest, or feeding without chicks, broods were considered to have failed. For calculating reproductive performance, I defined brood success as at least one chick surviving to 28 days post-hatch (Warriner et al. 1986). I captured and marked Snowy Plovers with the Florida Fish and Wildlife Conservation Commission (FWC) banding permit # 21980, and with approval from the University of Florida Animal Care and Use Committee (permit # 006-08WEC) .

Explanatory Variables

I analyzed four groups of explanatory variables that might influence selection and survival during the brood-rearing stage: physical features, human activity, prey availability, and predator activity. Each season I collected measurements at both nest and random point locations using three spatial scales: nest-site (1 m radius), nest-territory (100 m radius), and landscape scale (500 m radius).

Physical features of the habitat are thought to effect both selection and survival. In particular, brood survival is thought to depend upon cover from potential predators (Powell and Collier 2000); therefore I predicted a positive effect of increased vegetation, dunes, shell and organic debris. To test these predictions, I quantified the percent ground cover of vegetation, bare sand, shell debris, and organic debris at the nest-site. At the nest-territory I use a distance to object design (Williams et al. 2002), measuring the distance to vegetation, primary dune, dune height, and the distance to nearest conspicuous debris.

To test for the influence of human activity, I collected data at both the nest-territory and landscape scales. Because studies have documented greater brood survival in relation to low human disturbance (Cowell et al. 2007; Ruhlen et al. 2003), I predicted positive influences to selection and brood survival with the use of symbolic fencing and with increased distance from beach access points. Symbolic fencing is composed of signs and ropes and is often used by managers to protect nesting areas from human disturbance (see Lafferty 2001a). Within the nest-territory, I measured the presence/absence of beach access points, distance to nearest human foot print, and presence/absence of symbolic fencing within a 100 m radius. At the landscape scale, I systematically sampled human activity, predicting nest-site selection and survival to decrease as human density increased. To investigate the spatial variation in human disturbance potentially affecting nest-site selection and nest success, I quantified human density with beach foot traffic. I set up strip transects by raking 50 m long x 2 m wide sand transects running perpendicular from the shoreline to the primary dune line. Transects were set-up over the weekend to capture maximum beach activity levels and to investigate temporal variation, I conducted sampling twice during both breeding seasons. Sampling took place during the months of March and April early in the season and during June and July later in the breeding season.

To test for the influence of prey availability, I collected data at both the nest-territory and landscape scales. Loegering and Fraser (1995) documented higher piping plover survival rates for broods with access to high quality brood rearing-habitat; therefore, I predicted Snowy Plover broods would select for, and brood survival rates would be influenced by, foraging habitat type, with ephemeral pools positively influencing both selection and survival compared to other available foraging habitat types (Table 3-1). To test these predictions, within the nest-territory, I measured the distance from the nest to the nearest foraging habitat and identified the type of foraging habitat within a 100 m radius. Brood habitat selection for other plovers has been linked to the distribution of invertebrate prey (Whittingham et al. 2001; Pearce-Higgens and Yalden 2004). Therefore, at the landscape scale I systematically sampled prey availability by selecting a random point every 500 m of linear beach habitat based on grid system in ArcGIS. I categorized each habitat sampled into foraging habitat types and sampled epifaunal (surface-dwelling) invertebrates with pitfall traps and paint stirring sticks coated with Tanglefoot (The Tanglefoot Company; see Loegering and

Fraser 1995). I set up intertidal strip transects through random points running perpendicular from the shoreline to the vegetation line (see Smith and Faillace 2006). I arranged five sample arrays along a straight line between the low water mark and the foredune perpendicular to the shoreline. The first array was centered on the most recent wrack-line; the second array was at the highest wrack-line. The third array was centered at mid-beach, the fourth array was at the vegetation line and the fifth array was directly in front of the dune.

An array consisted of four pitfall traps made of clear plastic (diameter 11 cm, depth 8 cm) placed 2 m apart in a 2 m x 2 m plot and eight tangle foot sticks, two at each corner (one vertical and one horizontal). I placed each pitfall trap flush with the sand and filled each with 1 cm of H_20. Because wrack and vegetation are often correlated with invertebrate densities (Dugan et al. 2003), I recorded the percent vegetation and wrack cover at each array. After one hour, trap contents were collected and invertebrates were counted. To investigate annual variation in food availability, I sampled for invertebrates during July and August 2008 and 2009. These methods of prey sampling were appropriate because Snowy Plovers do not probe beneath the surface. Snowy Plovers employ a ‘picking’ feeding method using a ‘run-and-pause’ style based upon visual cues (Page et al. 2009).

To test the influence of predator activity, I collected data at both the nest-territory and landscape scales. Avian predators such as fish crows are often associated with forest patches. The forest patches located at these sites are composed primarily of slash pine (*Pinus elliottii*). Therefore, I recorded the presence/absence of the sand pine forest edge within a 100 m radius. Previous studies have documented ghost crabs predating plover chicks (Loegering et al. 1995; Himes et al. 2007). Thus, I measured to the nearest ghost crab burrow from the nest on hatch day. Beyond the perceived predator threat, I was interested in how the change in predator activity levels impacted survival based on predictions that selection and brood survival would decrease in response to increase predator densities. Therefore, at the landscape level I systematically sampled predator activity through tracking. I set up strip transects by raking 50 m long x 2 m wide sand transects running perpendicular from the shoreline to the primary dune line. Transects were sampled over a two-day period. Per transect, I counted the number of ghost crab burrows present, the number of observed predator tracks to account for other predator species (e.g., coyotes, raccoons, etc.), and the number of avian predators observed in the area (e.g., fish crows). To investigate potential temporal variation, I conducted index transects twice during both breeding seasons. Sampling took place during the months of March and April early in the season and during June and July later in the breeding season.

Brood-Site Selection

To test for brood-site selection, I created a grid with ArcGIS 9.2 by creating polygons of potential nesting habitat, based on aerial photographs and ground truthing. I identified potential nesting habitat as the sandy beach habitat located between the shoreline and tree-line or dense vegetation, incorporating much of the dunes. Within each polygon of potential nesting habitat, by site, I overlaid a grid (500 m x 500 m). I categorized each grid as either used or not with the presence of at least one foraging brood. I used the landscape-scale measurements to evaluate the influence of human activity, predator activity, and prey availability. To test the influence of physical features I used habitat variables that were measured during the invertebrate sampling (see above) such as the % wrack at the shoreline, % vegetation at the beach midline, and % vegetation at the foredune. I also categorized each grid by the presence of foraging habitat types. I classified grids as ephemeral or bay flats if one of these habitat types were present. If neither of these two foraging habitats were present, I classified the grid as shoreline foraging habitat.

Brood-Rearing Habitat Use

I quantified actual brood-rearing habitat use through an instantaneous sampling design by scanning for and recording all broods as they were encountered. To test whether foraging habitat type effected brood survival, I recorded each observed brood location with a Global Positioning System and recorded the type of brood-rearing habitat used. In addition, I calculated the distance traveled by broods from nesting area to brood-rearing area to test whether the proximity of foraging locations effected brood survival. For broods with multiple observations, I used the average distance traveled (Σ meters traveled / # of brood observations). Because predator, human, and invertebrate densities may differ at actual used areas, I calculated the landscape scale measurements (human, predator, and invertebrate counts) for the locations in which broods were observed foraging in addition to nest sites.

Statistical Analysis

Prey Availability

When collecting available prey items, I sampled foraging areas only at the end of the breeding season (i.e., July and August). In contrast, I recorded foraging habitat types as they were used by broods regardless of seasonal timing (April- August). Moreover, invertebrate densities often differ between foraging habitat types (Pearce-Higgens and Yalden 2004). Therefore, I was interested in whether invertebrate counts were in fact a product of foraging habitat type to eliminate issues of foraging habitats that were no longer available during the time of prey sampling (e.g., ephemeral pools that became dry but were available while broods were active). Invertebrate abundance represented count data and typically count data follow a Poisson distribution. However, for this data set, the variance was greater than the mean indicating a negative-binomial distribution was more appropriate. The data were modeled using Generalized Linear models (GLMs) with a negative-binomial distribution and log link function (Bliss and Fisher 1953). I included covariates collected during sampling such as site, date, wind, tide, weather and temperature.

Brood-Site Selection

To estimate brood-site selection, I used logistic regression to model the probability of selection as a function of the variables collected at the landscape scale (500 m grid) to represent my four *a priori* hypotheses. The response variable was whether or not at least one brood was observed foraging within each grid location. I used the binomial GLM procedure within R (2008) to estimate regression coefficients in the logistic models.

Brood Survival

On brood checks, I always located marked adult birds and determined whether each brood was active (i.e., with either the presence of chicks). I initially considered a Cormack-Jolly-Seber mark-recapture model (Williams et al. 2002) to estimate brood survival, but this method estimated a detection probability of 0.98. Consequently, I used the logistic-exposure method to model daily brood survival (Shaffer 2004). I used binomial GLMs within R (2008) to estimate regression coefficients in the logistic-exposure models. Using this method, I estimated brood daily survival rates from the resulting logistic function (Shaffer 2004). I used the effective sample size (n; Rotella et al. 2004) when analyzing model fit (i.e., n = total number of days that nests were known to survive + the total number of intervals in which a failure occurred) to adjust log-likelihoods in a model selection approach (see below). Between visits, the response variable was whether or not at least one chick per brood survived the interval.

Model Selection

Because I had many predictor variables (Table 3-2), I used a Spearman's non-parametric correlation matrix to check for potential multi-collinearity (Appendices C &D). After removing variables that were strongly correlated ($r>|0.6|$), I selected the best approximating model(s) using Akaike's Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002; Anderson 2008). For the brood survival models, total shell ground cover and sand ground cover were highly correlated ($r = 0.65$), so I dropped sand ground cover from further analysis because it is essentially the reciprocal of shell debris. Additionally, my predictions were based on benefits related to the presence of debris rather than the lack of debris (Powell and Collier 2000). Between scales, the distance to the nearest vegetation and the total vegetation ground cover at the nest were also highly correlated ($r = 0.78$), so I dropped the distance to the nearest vegetation because percent vegetation as an indicator of nest concealment has been used as a measure for many avian studies and percent vegetation catered more to my predictions.

After screening variables, I developed the most parsimonious model for explaining variation in brood-site selection or brood survival for each *a priori* hypothesis (prey availability, predator activity, human activity, and physical features) by using a manual forward model selection approach using AICc. The most parsimonious model for each hypothesis was then contrasted using AICc alongside a null (intercept-only) model. A model selection approach was useful here because it allows for simultaneously comparing different models that reflect biological hypotheses (Johnson and Omland 2004). Because these hypotheses are not mutually exclusive, I also explored the potential for these hypotheses to be operating in concert by considering additive effects of these hypotheses.

Results

Prey Availability

During both breeding seasons foraging habitat type, the level of wind, and weather at the time of sampling were important determinates of prey availability (Fig. 3-1a-c). Between the three available foraging habitats, ephemeral pools provided the highest amount of prey items (Fig. 3-1a).

Brood-Site Selection

The average distance broods traveled was 729 m, with a maximum distance traveled of 5.3 km. Therefore, the sampling of brood use within 500 m grids was an appropriate scale. Based on the data, there was some evidence for three *a priori* hypotheses with models representing prey availability, predator activity, and physical features fitting the data better than an-intercept only model (Table 3-3). However, the most parsimonious model contained only variables representing prey availability (Table 3-3). Specifically, broods selected habitat based on the type of foraging habitat present, where ephemeral pools were selected for at a greater probability than other available foraging habitats (Fig. 3-2).

Brood Survival

I monitored 202 broods comprising 367 chicks during the 2008-9 breeding seasons, resulting in an effective sample size of 3689 (see *Statistical Analysis*). The mean interval length between brood visits for both years was 6.4 days. I confirmed 147 total fledged chicks, resulting in an overall apparent fledge rate of 0.39 pooled across both years. Across years, the number of fledged chicks per successful brood averaged 1.37 ± 0.57 SD. At the brood level, I determined 64 (0.63) and 50 (0.48) nests to have fledged at least one chick during 2008 and 2009, respectively, resulting in a 0.55 apparent fledge rate pooled over both seasons.

The majority of chick mortality occurred during the first week post-hatch (Table 3-4). However, I could not document the cause for mortality because most chicks disappeared in between site visits. I was able to confirm five predation events observed opportunistically at the nest shortly after hatching. In all five cases ghost crabs were responsible for mortality. Additionally, one chick was predated by a ghost crab during trapping efforts. Fish crows and gull-billed terns were observed pursuing chicks and have been documented predating chicks in other plover studies (Himes et al. 2007; Page et al. 2009). However, they were sampled sporadically during tracking surveys, so I did not include them directly in any analyses. Based on predator sampling pooled across both seasons, I identified 6266 individual tracks. Of the total count, 92% represented ghost crab burrows (n = 5783). In comparison, only 5.2% of tracks were from coyotes (n = 324).

The best approximating model contained explanatory variables from three of the four *a priori* hypotheses, predator activity, prey availability, and physical features and each of these three fit better than the intercept-only model (Table 3-5). Broods were more likely to survive when foraging at ephemeral pools, in areas of low predator densities, with dunes backing the beach, and with greater debris around the nest (Fig. 3-3).

Discussion

Identification of habitat cues managers can utilize in the conservation of rare or declining species is critical for appropriate management. However, few avian habitat studies have been able to confront multiple ecological hypotheses for habitat selection, nor the fitness consequences of such decisions (Jones 2001) to aide in management decisions. While habitat selection is often assumed to be adaptive, evidence for adaptive habitat selection in birds has been mixed (Clark and Shutler 1999; Jones 2001).My results provide a unique illustration of how multiple selective forces influence brood-site selection and reproductive performance. Moreover, these results provide a clear example of adaptive offspring selection.

On the Florida Gulf Coast, differences in the distribution of prey availability influence habitat use by plover broods. In particular, the quality of foraging areas determined habitat selection. In addition to the distribution of prey availability, brood survival was influenced by a combination of predictors related to predator activity and physical features of the habitat. The influence in the spatial gradient of predator activity suggests that the quality of brood-rearing habitats was influenced by both food abundance and predation risk.

Prey Availability

Positive relationships between prey availability and brood survival rates have been reported for many avian species (Loegering and Fraser 1995; Elias et al. 2000; Pearce-Higgens and Yalden 2004). For precocial young, it is thought that low prey availability may slow development and chicks that fail to attain certain mass thresholds may not survive (Loegering and Fraser 1995; Le Fer et al. 2008). Well-fed chicks are more likely to cope with extreme temperatures and evade attacking predators (Kosztolanyi et al. 2007).

Plovers preferentially selected foraging habitats with greater counts of prey items. These preferences conferred a fitness advantage via greater probability of fledging at least one chick. In fact, the probability of fledging while foraging at ephemeral pools was more than twice that of broods foraging at other habitat types. Adaptive selection of high quality foraging habitat has been demonstrated in multiple avian studies (Smith and Dawkins 1971; Elias et al. 2000; Pearce-Higgens and Yalden 2004). Working with Great Tits (*Parus major*), Smith and Dawkins (1971) observed patterns of foraging area selection in relation to prey abundance. These birds allocated the greatest amount of time to areas of highest prey food abundance and progressively less time to worse areas. In addition to quality, the spatial heterogeneity of prey items has been documented as a determinate of species use patterns for many species (Goss-Custard 1984; Colwell and Landrum 1993; Ribeiro et al. 2004).

Theoretically, selection of foraging habitat should be the outcome of decisions that balance the trade-off between food abundance and predation risk (Frid and Dill 2002). For instance, Martin (1992) argued that life history traits (including fecundity) for many avian species are influenced by predation in combination with food limitation. Patterns in trade-offs have been observed across taxonomic groups including fish (e.g., Gilliam and Fraser 1987), ungulates (e.g., Berger 1991) small mammals (e.g., Morris and Davidson 2000), and sandpipers (Pomeroy 2006). In all examples listed, individuals spent less time in areas where high resource richness was associated with greater predation risk. In my study, bay tidal flats also provide a high level of invertebrate prey, but were rarely used for brood-rearing. In contrast to ephemeral pools, bay tidal flats are highly flat and open, with greater exposure to potential predators suggesting the existence of predator-sensitive foraging. To the contrary, I did observe a transition to bay tidal flats as broods fledged and during the onset of the wintering season by adults (pers. Obs.), demonstrating the influence of age-dependent predation pressures. Further examination between foraging habitats and predator pressures are clearly needed.

Physical Features And Predator Activity

The predation of young is often the primary source of reproductive failure cited across many taxa (Page et al. 1983; Angelstam 1986; Warriner et al. 1986; Martin 1992; Benson et al. 2010). Detailed analyses in this system suggested that brood survival was negatively correlated with predator abundance. Yet, in addition to the local abundance of predators, physical features of the habitat also influenced the probability of fledging. Differences in predation rates in relation to physical features of the habitat have been linked to varying foraging strategies of potential predators and the related cues they respond to in search of prey (Martin 1987; Soderstrom et al. 1998). Many studies have documented debris around nest sites to benefit survival by hindering the search image of potential predators (Cohen et al. 2008; Collins et al. 2009; Page et al. 2009). However, this is the first study to my knowledge that has linked debris as a positive influence on brood survival for species with mobile young (although it is often assumed; Powell 2001). Comparably, young plovers often respond to predators by seeking cover (Powell and Collier 2000; Colwell et al. 2007a) beneath vegetation, debris, or in the backing dunes. Although plovers typically leave the nest shortly after hatching, chick are more likely to die in the first hours after hatching than in subsequent time periods (Wolcott and Wolcott 1999; Colwell et al. 2007a). Consequently, debris and the backing dunes at the immediate nest site likely provide camouflage for chicks from potential predators.

The probability of fledging was related to predator abundance and ghost crabs were the most observed predator species. Because ghost crabs often respond to movement, they must taste objects to find stationary prey (Wolcott and Wolcott 1999). Therefore, a greater percentage of debris around the nest may confuse ghost crabs and decrease the probability of chick mortality. In addition, debris and dune cover likely provide protection from other potential terrestrial and avian predators.

Human Activity

In contrast with previous work in other regions (Ruhlen et al. 2003; Colwell et al. 2007a), human activity had little influence on brood-site selection or survival during this study. In California, Rhulen et al. (2003) observed disproportionate chick mortality over weekends, which presumably coincided with greater human activity. Colwell et al. (2007) observed lower chick survival on beach habitats, which maintained higher human activity levels, when compared to gravel bars. In both of these studies, human activity was never directly measured but assumed. The sites present in this study may have lower disturbance levels than those reported from California. I did observe differences in the amount of time required to reach a fully fledged state. In areas with the highest levels of human disturbance, broods were not observed as fully fledged until 35-42 days. Whereas in breeding locations around North America, the average age of fledging is 28 days (Warriner et al. 1986; Page et al. 2009). Additionally, several studies suggest that benefits during the nesting stage with protection from human disturbance (Lafferty et al. 2006; Lauten et al. 2007). However, current management efforts to lessen the impacts of human disturbance focus solely on nesting habitat. Therefore, I was not able to assess the potential influence of symbolic fencing on brood survival beyond the immediate nest site.

Conclusions

My results provide insight for management and conservation problems, because they show that one of the consequences of spatial variation in prey availability is that some beach areas are used by a greater number of Snowy Plovers than are other areas. Maintaining and creating high-prey foraging habitat, such as ephemeral pools, should thus be an important part of Snowy Plover management along the Florida gulf coast and likely for shorebird populations in other geographic regions. However, it is inevitable that the human population will continue to grow and the consequent disturbance and habitat alteration projects will also increase. Anthropogenic alteration projects, such as beach renourishment, are gaining popularity in most coastal habitats to combat beach erosion (Brown and McLachlan 2002), but beach renourishment may directly decrease prey availability for shorebirds (see Peterson and Bishop 2005; Peterson et al. 2006). Thus, given the increase use of coastal habitats as recreational sites, it will be important to continue to evaluate the influence of human impacts in relation to the spatial heterogeneity in prey availability and shorebird habitat use.

Much of the coastal beach habitats world-wide have been lost to development (Brown and McLachlan 2002; Dugan and Hubbard 2006). The loss of beach habitat continues at an alarming rate and as a consequence shorebird populations’ continue to decline (Burger 2000). Conservationists have responded by protecting shorebird nesting areas in many locations where breeding still occurs. However, monitoring, management and estimation of brood survival rarely occur. This study stresses the habitat requirements relevant to the brood-rearing stage of breeding shorebirds. Broods were susceptible to changes in predator abundance. However, the predator community impacting brood survival in Florida is vastly different than what has been reported in other regions. Management efforts should likewise focus on the predator community responsible for local mortality. In addition, this study highlights the importance of prey availability and more importantly access to high quality foraging habitat. Conservation of shorebirds will require management of brood-rearing habitat in addition to current efforts associated with nesting and should include considerations for both predator activity and prey availability in addition to physical features of the habitat. Additional monitoring and demographic studies are necessary to determine the utility of alternative management regimes to ensure persistence of these populations.

Table 3-1. Brood foraging habitat types of the Gulf Coast of Florida

Habitat Type*	Distinguishing features
Ephemeral pool	Low energy, standing water pool with surrounding moist sand. Typically with sparse to medium vegetation, but backed by dunes with denser vegetation. Standing water derives from either high tide or storm activity due to the presence of low dips located between the shoreline and dune line.
Bay tidal flat	Mud flats submerged only at high tide. Are generally only reached by waves of low amplitude, resulting in moist sand. Typically sparsely vegetation, flat, and exposed. Some salt-tolerant plants (mostly *Salicornia* and *Spartina*).
Shoreline	High to medium energy wave dominated. Moist sand limited to the swash zone, where waves are projected up the beach slope. Typically with standing wrack (largely composed of dead marsh grass) and sparse vegetation, but backed by dunes with dense vegetation. Includes both the gulf or bay shorelines. Foraging restricted to between the shoreline and foredune.

* Habitat type definitions modified from Davis and Fitzgerald (2004)

Table 3-2. Explanatory variables considered in the analysis of Snowy Plover Brood-site selection and survival, Gulf Coast of Florida, 2008–2009

Variable	Description
Physical Features	
Vegetation *	Percent vegetation cover at 1 m radius
Sand*	Percent sand cover at 1 m radius
Debris*	Percent debris cover at 1 m radius
DistVegetation*	Distance (m) to the nearest vegetation within 100 m radius
DistDune*	Distance (m) to the nearest dune within 100 m radius
DuneHgt*	Height (m) of the nearest dune
Distdebris*	Distance (m) to the nearest conspicuous debris within 100 m radius
Wrack**	Percent wrack cover at sampling points at 500 m scale
MidVeg**	Percent vegetation cover at midbeach sampling points at 500 m scale
DuneVeg**	Percent vegetation cover at foredune sampling points at 500 m scale
Prey Availability	
DistWater*	Distance (m) to the nearest foraging habitat within 100 m radius
TypeForaging*	Nearest foraging habitat type to nest
Foraging	Presence of foraging habitat type at 500 m
Distance*	Distance (m) travelled by brood from nest to foraging habitat
ForagingUsed*	Foraging habitat used by broods
Predator Activity	
Forest*	Distance (m) to the nearest forest patch within 100 m radius
GhostCrab*	Distance (m) to the nearest ghost crab burrow within 100 m radius
Predator	Total count of observed predator tracks at 500 m
Human Activity	
Fencing*	Presence/absence of symbolic fencing within 100 m radius
Access*	Presence/absence of beach access points within 100 m radius
HumanPrint*	Distance (m) to the nearest human footprint within 100 m radius
Human	Total count of observed human tracks at 500 m

*Variables considered only in brood survival models

**Variables considered only in brood-site selection models

Table 3-3. Brood-site selection models based on a priori hypotheses for Snowy Plovers (n=451) on the Gulf Coast of Florida, 2008, 2009. Models are ranked based on Akaike's Information Criterion for small samples (AICc), AICc is based on -2LL, which is the value of the maximized log-likelihood function of the model parameters given the data set, the number of parameters (K), and Δ AICc is the AICc differences relative to the smallest AICc in the model set.

Hypothesis*	K	AICc	-2LL
Physical Features			
Wrack	2	555.71	-551.68
Prey Availability			
Foraging	3	485.41	-479.36
Predator Activity			
Predator	2	556.97	-552.94
Human Activity			
Human	2	559.11	-555.08
Intercept Only	1	559.14	-557.14
*Best Additive Model***			
Foraging	3	485.41	-479.37

*Wrack= % standing wrack at sampling area, Foraging= type of foraging habitat present, Predator=predator density counts (500 m), Human= human density counts (500 m).

**Best Additive Models include those < 2 ΔAICc from the best model.

Table 3-4. Number of chicks present from hatch to fledging by week, rows 1-4 represent week in age of survival.

Week	2008	2009	Total	Mortality*
0**	199	168	367	-
1	128	87	215	0.69
2	94	60	154	0.28
3	93	55	148	0.05
4	92	55	147	0.00

*Mortality = total lost from previous week to current week divided by the total number of chicks lost during the study

**0 = day of hatching

Table 3-5. Brood survival models based on *a priori* hypotheses for Snowy Plovers (n=202) on the Gulf coast of Florida, 2008, 2009. Models are ranked based on Akaike's Information Criterion for small samples (AICc), AICc is based on -2LL, which is the value of the maximized log-likelihood function of the model parameters given the data set, the number of parameters (K), and Δ AICc is the AICc differences relative to the smallest AICc in the model set.

Hypothesis*	K	AICc	-2LL
Physical Features			
DuneHgt+Debirs	3	494.06	-488.06
Prey Availability			
Foraging	3	476.77	-470.78
Predator Activity			
Predator	2	494.83	-490.82
Human Activity			
Human	2	500.02	-496.02
Intercept Only			
	1	498.85	-496.85
Best Additive Model			
DuneHgt+Shell+Foraging+Predator	6	465.17	-453.14

*DuneHgt= the height of the nearest primary dune (100 m), Debris= % shell and organic debris located around the immediate nest (1 m), Foraging= type of foraging habitat used by broods, Predator= density of predators (500 m) around the nest site, and Human= density of human beach traffic (500 m) around the nest site.

**Best Additive Models include those < 2 ΔAICc from the best model.

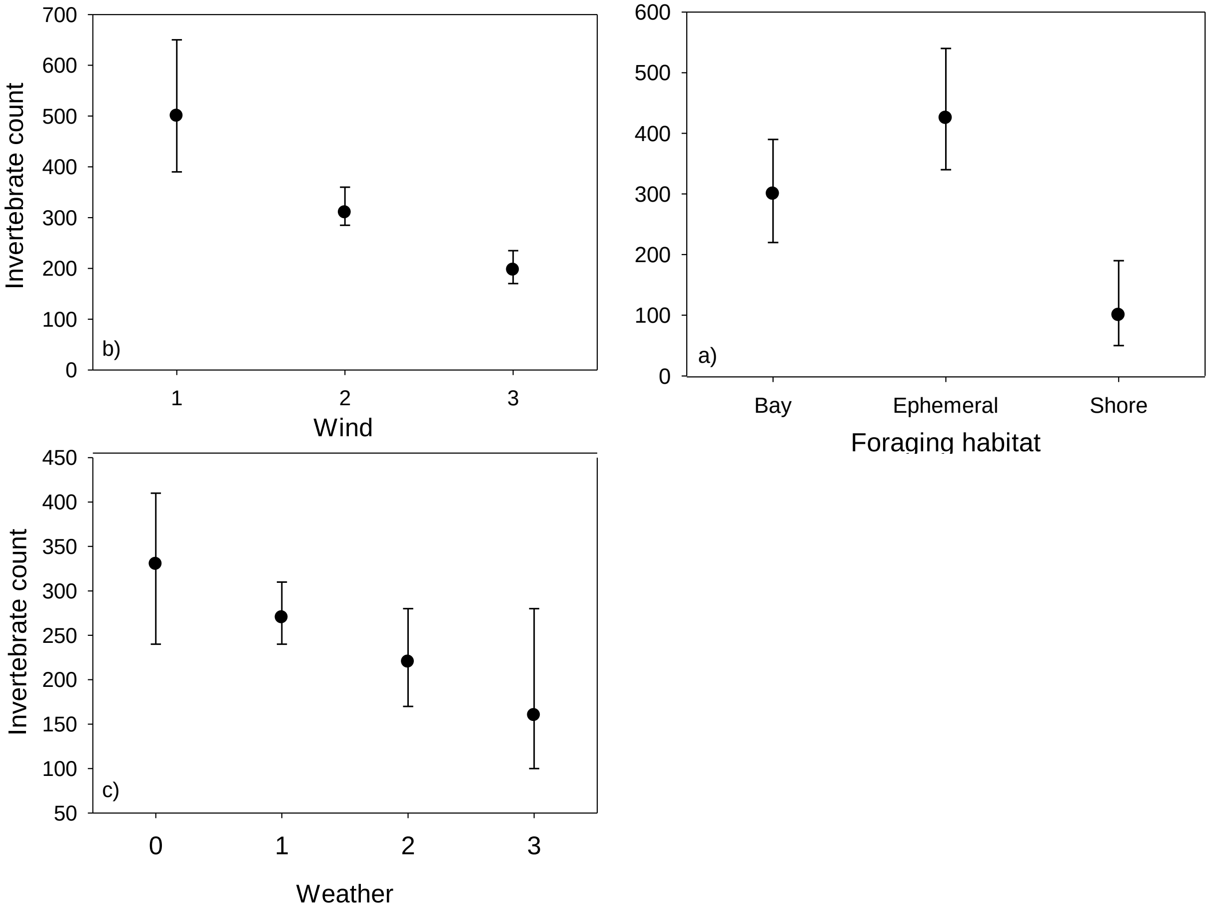

Figure 3-1. Predictors influencing invertebrate counts, a)foraging habitat type at sampling location, b) Beaufort wind codes: 1= 1-3 mph, 2= 4-7 mph, 3= 8-12 mph, c) weather codes: 0= clear, 1= partly cloudy, 3= drizzle.

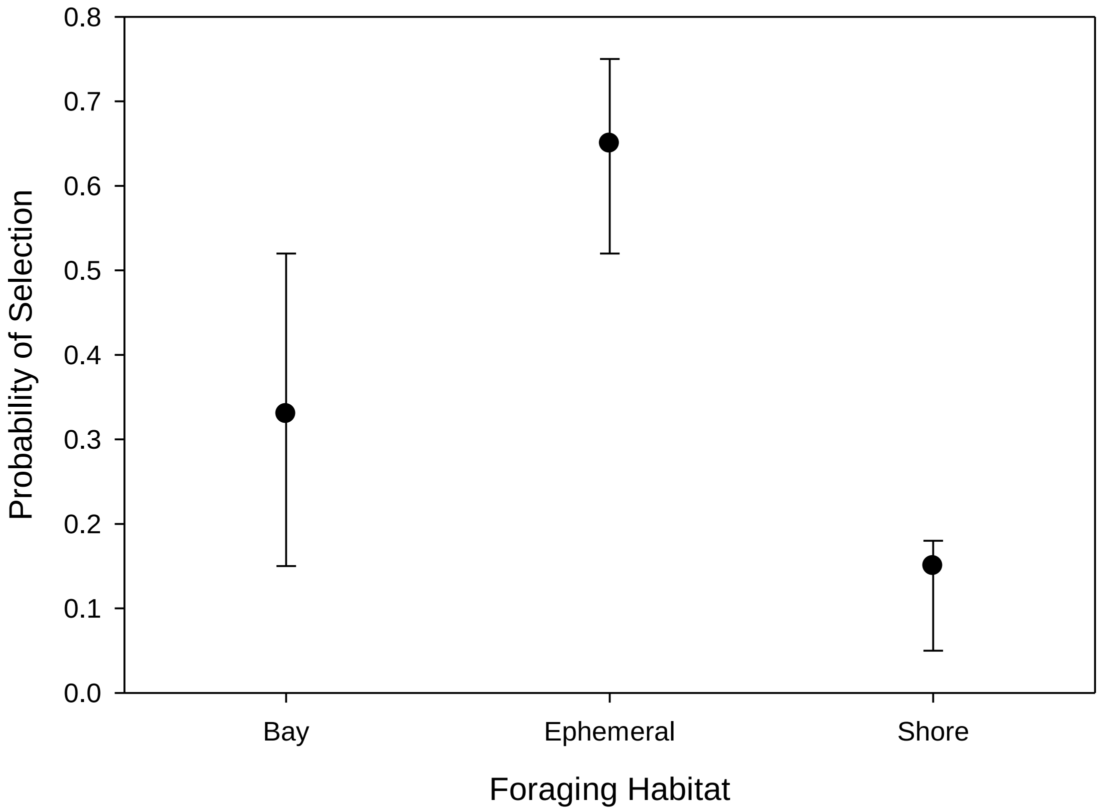

Figure 3-2. The probability of Snowy Plover Brood-Site Selection as a function of foraging habitat type based on the most parsimonious model, with 95% confidence limits on the Gulf coast of Florida, 2008, 2009.

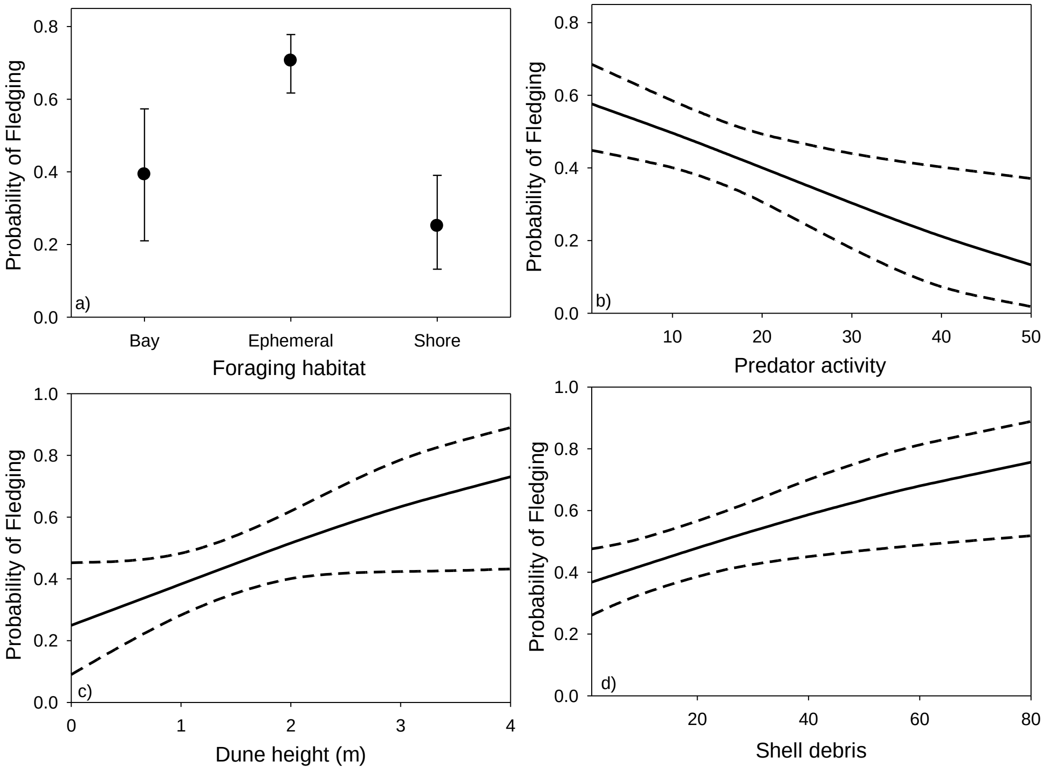

Figure 3-3. The probability of Snowy Plovers fledgling at least one chick (28 day period) as a function of predictors from the most parsimonious model(s) with 95% confidence limits, a) foraging habitat type used for brood-rearing, b) predator counts within 500m, c) dune height (m) within 100m radius, d) % debris at the immediate nest site within a 1m radius on the Gulf coast of Florida, 2008, 2009.

CHAPTER 4
SYNTHESIS, MANAGEMENT AND RECOMMENDATIONS FOR FUTURE RESEARCH

During both nesting and brood-rearing stages of breeding, Snowy Plover selection of habitat and productivity are influenced by a combination of factors including human disturbance, predator abundance, prey availability and the physical features of the habitat. However, there were marked distinctions in the factors influencing the two breeding stages (nesting and brood-rearing). Differences are not surprising, given the differences in mobility between stages (i.e., sessile vs. mobile). The impacts of human disturbance provided the greatest dichotomy between these two stages of breeding.

Human Disturbance

Symbolic fencing. This study documented increased probability of nest-site selection and a resulting benefit in terms of nest survival with the presence of symbolic fencing to prevent the impacts from human disturbance. However, I observed little direct influence from the impacts of human activity. However, current efforts to minimize the impacts of human disturbance through symbolic fencing are limited to nest sites. It may be possible to improve brood survival rates with the placement of symbolic fencing around high quality brood-rearing areas such as ephemeral pools and bay tidal flats (where brood survival rates were lower but could be higher based on prey availability). Posting of ephemeral pools will likely improve brood survival, but will additionally contribute to nest survival. Nest-site selection was positively influenced by the presence of ephemeral pools; however nests in close proximity to foraging habitat were less likely to hatch. Therefore, the placing of fencing around this habitat type will likely improve the nesting habitat as well and limit the distance travelled by individual broods. However, predatory birds have been observed using fencing materials for perching. Therefore, future research on the benefits of protecting brood-rearing habitats should be conducted before the wide-scale use of symbolic fencing at all foraging habitats. Additionally, further work with direct human disturbance is needed to determine the spatial extent of disturbance under varying background disturbance levels. Such research with disturbance will determine the spatial buffers needed for the placement of symbolic fencing under different disturbance levels throughout Florida and other regions of North America.

Pet disturbance. Pets, particularly dogs, are prohibited by law on most public beaches in Florida. However, pets are extremely common on beaches. In fact, there has been a growing trend towards the establishment of dog parks, as well as dog owners that do not abide by existing dog restrictions, and a lack of adequate enforcement of those restrictions. Birds are particularly sensitive to disturbance by dogs. This sensitivity is illustrated by observations that Snowy Plovers react at twice the approach distance by dogs than by pedestrians (Lafferty 2001a). Although pets do not remove habitat or necessarily kill birds directly, disturbances cause birds to suspend feeding and/or expend energy while in flight, moving on the ground, or maintaining vigilance (Burger 1994; Lafferty 2001a), and may directly result in loss of eggs and chicks due to exposure. Further research is needed to determine the spatial extent of disturbance and to quantify whether such disturbances have effects on the reproductive performance of Snowy Plovers.

Chick development. Although my study showed little influence of human activity on brood survival, I observed differences in the amount of time required to reach a fully fledged state. In areas with the highest levels of human disturbance, broods were not observed as fully fledged until 35-42 days. Whereas in breeding locations around North America, the average age of fledging is 28 days (Warriner et al. 1986; Page et al. 2009). Although I collected mass and tarsus length at hatch day, these measurements had no influence on the probability of fledging or with the level of human disturbance at each of the nesting sites. Researchers documented a relationship between growth and prey availability through capturing and measuring chicks on a weekly basis (Kosztolanyi et al. 2007). A similar approach with chick development in relationship to human disturbance would aid in understanding the impacts of human activity in chick growth.

Beach renourishment. Currently, anthropogenic alteration projects (e.g. beach renourishment) are popular in most coastal habitats to combat beach erosion (Brown and McLauchlan 2002). However, based on the findings of this study, such practice is likely detrimental to brood survival. During the process of renourishment, sand from the sea floor is dumped on the beach surface. Post-renourished beaches are typically composed of bare sand with very little organic or shell debris. The reduction in availability of beach debris may negatively influence survival by reducing chick concealment from potential predators. In addition, current renourishment practices impact prey availability in two ways. Prey availability tends to decline temporarily directly after renourishment (Dugan and Hubbard 2006; Peterson et al. 2006). More importantly however, in this system, ephemeral pools were both selected for and positively influenced survival. These pools are created from low dips located between the shoreline and dune line (Davis and Fitzgerald 2004). Renourishment typically results in level flat beaches decreasing the probability of ephemeral pool formation. At altered beach sites, maintaining and creating high-prey foraging habitat, such as ephemeral pools, should be an important part of Snowy Plover management along the Florida gulf coast and likely for plover populations in other geographic regions. Thus, monitoring the consequences of such engineering activities and the potential impacts to foraging habitat availability is of general interest to the conservation of shorebirds in coastal habitats.   Secondarily, the development of techniques to create high quality brood-rearing habitat in connection with current beach renourishment projects is needed.

Sea turtle surveys. Management for one species does not always positively benefit others species present in a given habitat. Snowy Plover nest survival was negatively influenced by beach width (i.e. distance from shoreline to nest). Turtle surveyors on ATVs use the shoreline for daily nest monitoring and ATV use in close proximity to nests often leads to a greater frequency of flushing. On most Florida beaches surveys take place daily from May to October (J. Mitchell pers Com.), during large portions of the Snowy Plover breeding season. The impact to shorebirds and seabirds of these intensive surveys is currently unknown. Turtle surveys typically take place between sunset and 10 am (J. Mitchell pers Com.), overlapping the time for which ghost crabs are primarily active (Wolcott and Wolcott 1999). It is possible that predation occurs because of the timing of which plovers are flushed from the nest. Consequently, they are most susceptible to ghost crab predation because crabs are more likely to be active. Unfortunately, in this study we were unable to test the influence of turtle surveys because surveying occurred at all sites equally. However, I did observe ATV tracks from turtle surveys less than 1 m from unmarked active nests on more than one occasion. In addition, Epstein (1999), while monitoring sea turtles, observed less direct impacts to marked Wilson's plover nests. However, this same study observed mortality of chicks that were crushed via ATVs. Chicks are mobile and therefore cannot be marked to inform turtle surveyors of their locations. Further research on the potential impacts to other coastal species from current sea turtle surveys is needed. In addition, education and coordination between managers, researchers, and surveyors of all coastal species is essential for conservation of coastal-dependent species.

Predator Activity

This study highlighted a unique and important predator for Snowy Plovers, apparently unique to the Florida population, the ghost crab. Ghost crabs influenced nest-site selection and nest and brood survival. Although, it seems clear that ghost crabs are impacting Snowy Plover habitat use and productivity, the mechanisms underlying this interaction are unclear. Without knowledge of the mechanisms resulting in predation, it is impossible to manage for the impacts related to ghost crabs. Further work with ghost crab predation and human disturbance stimuli is needed.

The relationship between human disturbance and ghost crab densities has led to many contradictory results. Some research says there is a negative relationship in crab numbers in relation to human disturbance (Barros 2001; Neves and Bemvenuti 2006). Other studies suggest an increase in crab numbers due to the garbage and food remains left by beach-goers (Strachan et al. 1999). It is possible that there are many thresholds in both human and ghost crab densities that when combined impact plover productivity. For example, sites located in peninsular Florida (e.g., Sanibel Island) exhibit high fledge rates at areas with very high human disturbance levels (Smith and Faillace 2006). However, ghost crabs are essentially absent at these sites due to high human disturbance (B. Smith pers Com.). At the other end of the spectrum, sites with very little human disturbance (e.g., St. Vincent NWR) had low occurrence of ghost crab depredation events although ghost crab densities were similar to surrounding sites. It appears that plovers are impacted at locations where high ghost crab and human densities overlap.

Predator removal programs may have unforeseen consequences for nesting beaches by impacting the community structure (Stapp 1997). For example Barton and Roth (2008) observed greater numbers of sea turtle nests depredated by ghost crabs after raccoons were removed. At many coastal beach habitats extensive predator control programs are in place in efforts to protect sea turtle nests. However, rarely are the predator communities evaluated before or after control efforts. Therefore, the benefits from predator control and the potential impacts to other coastal beach species (e.g., shorebirds, beach mice) remain unclear. Because ghost crabs can reach high densities in the absence of heavy predation (Burggren and McMahon 2009), predator removal experiments should be conducted to determine if current predator removal efforts are effective for shorebirds, seabirds, and sea turtle productivity on Florida’s Gulf Coast beaches. Additionally, because ghost crabs are far too numerous to control and there appears to be an interaction between human disturbance stimuli and ghost crab depredation, the protection of habitat from human disturbance would likely have the most influential impact in preventing ghost crab predation.

Beyond Productivity

Based on the results of this study, we now have broad-scale estimates for hatch and fledge rates for Snowy Plovers nesting in Florida, but juvenile survival rates and adult survival remain unknown. Such information is necessary for estimating population growth rates and understanding the ability of these populations to persist into the future.

Based on past state-wide counts since 1989, the plover population has changed very little (Himes et al. 2007). However, based on the current hatch and fledge rates, we should expect an increase in the breeding population. Either birds are dispersing outside of the state or survival during the juvenile stage is impacting the adult breeding population. However, during the course of this study, juvenile return rates were relatively high (45.6%) and were comparable to natal return rates observed for Snowy Plovers in other geographic locations (see Colwell et al. 2007b; Lauten et al. 2007)

The hatch rates observed in this study were influenced by the protection of nests from human disturbance. However, wide-scale management to protect nesting habitat from human disturbance has only been conducted over the past five years. In addition, periodic hurricanes may have an impact on both juvenile and adult survival. Despite the impacts from hurricanes on Florida’s coastline, there has been little attention focused on how these impacts influence shorebird survival. Continuation of banding and resighting efforts is needed in Florida to determine juvenile and adult survival and to tease apart these potential influences.

Winter dispersal And Habitat Requirements

Study of the migration and winter destinations of Snowy Plovers in Florida and the rest of the southeast are required to clarify where interior and coastal populations spend the non-breeding season (Himes et al. 2007). The monitoring of currently marked individuals during the winter will allow for determination of non-breeding movements and determination of whether the Florida population is a resident or migratory between breeding seasons. Monitoring during the winter season will also provide a better understanding of winter habitat requirements for plovers and other shorebirds. During the breeding season I observed consistent use of ephemeral pool foraging habitats.

However, I also observed a shift in increasing use of bay tidal flats upon fledging. The potential shift in habitat use post-breeding is currently unclear. Conservation of this species and other coastal breeders will require understanding and management of both breeding and wintering habitat requirements.

The Florida panhandle serves as an important breeding area for Snowy Plovers and provides one of the last large contiguous tracts of breeding habitat available to them in this region (Himes et al. 2007). With this study I illustrated the influence of human activity, predator activity, prey availability and physical features of the habitat on Snowy Plover site selection and survival during nesting and brood-rearing stages. Continued efforts to advance our understanding of habitat requirements, long-term survival and the influence of direct human disturbance are necessary in order to expand effective methods for management and conservation of Snowy Plovers and other shorebird species.

APPENDIX A
SPEARMAN'S RANK NON-PARAMETRIC CORRELATION MATRIX FOR VARIABLES INCLUDED IN NEST-SITE SELECTION MODELS

	Fencing	DistVeg	Veg	Sand	Debris	DistWater	DistDune	TypeForaging	Forest
Fencing	1.00	-0.08	-0.02	-0.23	0.27	0.18	-0.01	-0.24	-0.11
Distveg	-0.08	1.00	-0.87	0.42	0.29	-0.41	0.39	0.19	-0.03
Veg	-0.02	-0.87	1.00	-0.39	-0.46	0.33	-0.30	-0.14	0.10
Sand	-0.23	0.42	-0.39	1.00	-0.33	-0.27	0.12	0.19	0.02
Debris	0.27	0.29	-0.46	-0.33	1.00	-0.08	0.13	-0.11	-0.21
DistWater	0.18	-0.41	0.33	-0.27	-0.08	1.00	-0.29	0.06	0.00
DistDune	-0.01	0.39	-0.30	0.12	0.13	-0.29	1.00	0.03	-0.04
TypeForaging	-0.24	0.19	-0.14	0.19	-0.11	0.06	0.03	1.00	0.23
Forest	-0.11	-0.03	0.10	0.02	-0.21	0.00	-0.04	0.23	1.00
DuneHgt	-0.21	0.06	0.01	0.09	-0.18	-0.03	0.03	0.17	0.10
Distdebris	-0.24	0.21	-0.07	0.39	-0.31	-0.26	0.13	0.22	0.24
Ghostcrab	0.21	0.00	-0.12	-0.13	0.28	0.24	0.03	-0.15	-0.13
Access	0.24	0.02	0.04	-0.08	0.02	-0.06	0.10	-0.33	-0.24
DistHuman	0.08	-0.27	0.21	-0.18	-0.08	0.46	-0.13	-0.13	0.10
Predtracks	-0.04	0.05	-0.02	0.10	-0.10	-0.08	0.01	0.14	0.10
Human	0.16	-0.05	0.08	-0.03	-0.02	-0.03	0.01	-0.11	-0.12
Foraging	0.18	-0.13	0.07	-0.10	0.06	0.08	-0.03	-0.32	-0.22

	DuneHgt	DistDebris	GhostCrab	Access	DistHuman	Predator	Human	Foraging
Fencing	-0.21	-0.24	0.21	0.24	0.08	-0.04	0.16	0.18
Distveg	0.06	0.21	0.00	0.02	-0.27	0.05	-0.05	-0.13
Veg	0.01	-0.07	-0.12	0.04	0.21	-0.02	0.08	0.07
Sand	0.09	0.39	-0.13	-0.08	-0.18	0.10	-0.03	-0.10
Debris	-0.18	-0.31	0.28	0.02	-0.08	-0.10	-0.02	0.06
Distwater	-0.03	-0.26	0.24	-0.06	0.46	-0.08	-0.03	0.08
DistDune	0.03	0.13	0.03	0.10	-0.13	0.01	0.01	-0.03
TypeForaging	0.17	0.22	-0.15	-0.33	-0.13	0.14	-0.11	-0.32
Forest	0.10	0.24	-0.13	-0.24	0.10	0.10	-0.12	-0.22
HgtDune	1.00	0.11	-0.11	-0.11	0.00	0.19	-0.07	-0.05
Distdebris	0.11	1.00	-0.27	0.01	-0.23	0.03	-0.01	-0.16
Ghostcrab	-0.11	-0.27	1.00	0.07	0.10	-0.11	-0.02	0.14
Access	-0.11	0.01	0.07	1.00	-0.20	-0.19	0.17	0.22
DistHuman	0.00	-0.23	0.10	-0.20	1.00	0.05	-0.22	0.11
Predator	0.19	0.03	-0.11	-0.19	0.05	1.00	0.15	-0.10
Human	-0.07	-0.01	-0.02	0.17	-0.22	0.15	1.00	-0.09
Foraging	-0.05	-0.16	0.14	0.22	0.11	-0.10	-0.09	1.00

APPENDIX B
SPERMAN’S RANK NON-PARAMETRIC CORRELATION MATRIX FOR VARIABLES INCLUDED IN NEST SURVIAL MODELS

	Posted	Veg	Sand	Debris	DistWater	TypeForaging	DistDune	DuneHgt
Posted	1.00	-0.07	-0.09	0.16	0.01	-0.15	0.17	-0.14
Veg	-0.07	1.00	0.00	-0.52	-0.04	-0.13	-0.23	-0.02
Sand	-0.09	0.00	1.00	-0.61	0.08	0.04	-0.08	0.15
Debris	0.16	-0.52	-0.61	1.00	-0.06	0.00	0.28	-0.14
DistWater	0.01	-0.04	0.08	-0.06	1.00	0.38	-0.03	-0.05
TypeForaging	-0.15	-0.13	0.04	0.00	0.38	1.00	-0.03	0.13
DistDune	0.17	-0.23	-0.08	0.28	-0.03	-0.03	1.00	-0.10
DuneHgt	-0.14	-0.02	0.15	-0.14	-0.05	0.13	-0.10	1.00
Forest	0.05	0.00	0.10	-0.11	0.20	0.17	-0.06	-0.01
DistVeg	0.11	-0.78	-0.03	0.45	-0.03	0.06	0.26	0.08
DistDebris	0.21	0.08	-0.01	-0.01	0.03	0.01	-0.03	-0.01
GhostCrab	0.04	-0.18	-0.01	0.12	0.14	-0.05	0.22	-0.09
Access	0.46	0.06	-0.14	0.07	0.01	-0.29	0.17	-0.11
DistHuman	-0.12	0.03	0.11	-0.08	0.22	-0.06	-0.06	0.02
Predator	0.00	-0.05	0.13	-0.13	-0.18	0.11	-0.05	0.20
Human	0.18	0.03	0.06	-0.05	-0.10	-0.11	-0.03	0.00
Foraging	0.00	0.08	0.04	-0.06	-0.06	-0.27	0.08	-0.05

	Forest	DistVeg	DistDebris	GhostCrab	Access	DistHuman	Predator	Human	Foraging
Posted	0.05	0.11	0.21	0.12	0.46	-0.12	0.00	0.18	0.00
Vegetation	0.00	-0.78	0.08	-0.18	0.06	0.03	-0.05	0.03	0.08
Sand	0.10	-0.03	-0.01	0.03	-0.14	0.11	0.13	0.06	0.04
Shell	-0.11	0.45	-0.01	0.14	0.07	-0.08	-0.13	-0.05	-0.06
Distwater	0.20	-0.03	0.03	0.11	0.01	0.22	-0.18	-0.10	-0.06
Typewater	0.17	0.06	0.01	0.02	-0.29	-0.06	0.11	-0.11	-0.27
Distdune	-0.06	0.26	-0.03	0.13	0.17	-0.06	-0.05	-0.03	0.08
Dunehgt	-0.01	0.08	-0.01	-0.05	-0.11	0.02	0.20	0.00	-0.05
Forest	1.00	-0.01	0.19	0.02	-0.10	0.12	0.08	-0.03	-0.15
Distveg	-0.01	1.00	-0.07	0.17	0.04	-0.03	0.09	-0.04	-0.05
Distdebris	0.19	-0.07	1.00	0.06	0.02	-0.03	-0.09	0.01	-0.08
crabfirst	0.07	0.20	0.03	0.17	0.16	0.07	-0.13	-0.03	0.08
Access	-0.10	0.04	0.02	0.06	1.00	-0.16	-0.14	0.07	0.25
human	0.12	-0.03	-0.03	-0.07	-0.16	1.00	0.06	-0.18	0.07
Pred	0.08	0.09	-0.09	0.00	-0.14	0.06	1.00	0.26	-0.08
Tracks	-0.03	-0.04	0.01	-0.03	0.07	-0.18	0.26	1.00	-0.17
Foraging	-0.15	-0.05	-0.08	0.01	0.25	0.07	-0.08	-0.17	1.00

APPENDIX C
SPEARMAN'S RANK NON-PARAMETRIC CORRELATION MATRIX FOR VARIABLES INCLUDED IN BROOD-SITE SELECTION MODELS

	Human	Predator	Invert	MidVeg	Wrack	DuneVeg	Foraging
Human	1.00	0.14	0.00	-0.19	-0.01	-0.18	-0.10
Predator	0.14	1.00	-0.15	-0.06	-0.07	0.09	0.13
Invert	0.00	-0.15	1.00	0.09	0.27	0.00	-0.49
MidVeg	-0.19	-0.06	0.09	1.00	0.12	0.29	-0.10
Wrack	-0.01	-0.07	0.27	0.12	1.00	0.14	-0.17
DuneVeg	-0.18	0.09	0.00	0.29	0.14	1.00	0.09
Foraging	-0.10	0.13	-0.49	-0.10	-0.17	0.09	1.00

APPENDIX D
SPEARMAN’S RANK NON-PARAMETRIC CORRELATION MATRIX FOR VARIABLES INCLUDED IN BROOD SURVIVAL MODELS

	Posted	Veg	Sand	Debris	DistWater	TypeForaging	DistDune	DistVeg	DuneHgt
Posted	1.00	-0.03	-0.10	0.16	-0.03	-0.12	0.16	0.09	-0.15
Veg	-0.03	1.00	0.05	-0.50	-0.06	-0.13	-0.23	-0.79	0.07
Sand	-0.10	0.05	1.00	-0.65	0.15	0.05	-0.14	-0.07	0.23
Debris	0.16	-0.50	-0.65	1.00	-0.12	-0.04	0.32	0.40	-0.27
DistWater	-0.03	-0.06	0.15	-0.12	1.00	0.52	-0.07	-0.06	-0.02
TypeForaging	-0.12	-0.13	0.05	-0.04	0.52	1.00	0.00	0.06	0.07
DistDune	0.16	-0.23	-0.14	0.32	-0.07	0.00	1.00	0.27	-0.05
DistVeg	0.09	-0.79	-0.07	0.40	-0.06	0.06	0.27	1.00	0.07
DuneHgt	-0.15	0.07	0.23	-0.27	-0.02	0.07	-0.05	0.07	1.00
Forest	0.12	-0.03	0.14	-0.11	0.28	0.17	-0.03	-0.02	-0.06
DistDebris	0.24	0.09	0.01	-0.02	-0.02	-0.06	-0.06	-0.11	0.04
GhostCrab	0.06	-0.29	0.01	0.24	0.10	0.07	0.14	0.28	-0.06
Access	0.48	0.08	-0.11	0.05	0.05	-0.12	0.07	-0.03	-0.08
DistHuman	-0.13	0.04	0.19	-0.15	0.13	-0.07	0.01	-0.10	-0.06
Foraging	0.06	-0.01	0.16	-0.17	-0.15	-0.22	-0.02	0.02	0.14
Distance	-0.14	0.04	0.04	-0.09	0.08	0.18	-0.25	-0.03	0.17
Human	0.29	0.16	-0.15	0.13	-0.04	-0.24	0.02	-0.13	-0.30
Predator	-0.15	0.03	0.17	-0.19	-0.13	-0.09	-0.16	-0.03	0.15

	Forest	DistDebris	GhostCrab	Access	DistHuman	Foraging	Distance	Human	Predator
Posted	0.12	0.24	0.06	0.48	-0.13	0.06	-0.14	0.29	-0.15
Veg	-0.03	0.09	-0.29	0.08	0.04	-0.01	0.04	0.16	0.03
Sand	0.14	0.01	0.01	-0.11	0.19	0.16	0.04	-0.15	0.17
Debris	-0.11	-0.02	0.24	0.05	-0.15	-0.17	-0.09	0.13	-0.19
DistWater	0.28	-0.02	0.10	0.05	0.13	-0.15	0.08	-0.04	-0.13
TypeForaging	0.17	-0.06	0.07	-0.12	-0.07	-0.22	0.18	-0.24	-0.09
DistDune	-0.03	-0.06	0.14	0.07	0.01	-0.02	-0.25	0.02	-0.16
DistVeg	-0.02	-0.11	0.28	-0.03	-0.10	0.02	-0.03	-0.13	-0.03
DuneHgt	-0.06	0.04	-0.06	-0.08	-0.06	0.14	0.17	-0.30	0.15
Forest	1.00	0.20	0.02	-0.05	0.12	-0.07	-0.10	-0.05	-0.08
DistDebris	0.20	1.00	0.03	0.07	0.03	0.14	-0.02	-0.01	-0.07
GhostCrab	0.02	0.03	1.00	0.06	-0.16	-0.03	-0.11	0.07	-0.01
Access	-0.05	0.07	0.06	1.00	-0.14	-0.05	0.02	0.27	-0.15
DistHuman	0.12	0.03	-0.16	-0.14	1.00	0.15	-0.14	-0.26	0.02
Foraging	-0.07	0.14	-0.03	-0.05	0.15	1.00	-0.10	-0.16	0.10
Distance	-0.10	-0.02	-0.11	0.02	-0.14	-0.10	1.00	-0.03	0.00
Human	-0.05	-0.01	0.07	0.27	-0.26	-0.16	-0.03	1.00	-0.17
Predator	-0.08	-0.07	-0.01	-0.15	0.02	0.10	0.00	-0.17	1.00

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BIOGRAPHICAL SKETCH

Raya Pruner grew up in a rural timber town, with a population little more than 3000, in SW Oregon. When she wasn't in school, she spent most of her childhood outdoors. She graduated in 2002 from the University of Montana with two degrees, one in wildlife biology and one in archaeology. At that time she had become fascinated with the Pleistocene megafauna extinctions. However, she was hired the following year by the Bear River Migratory Bird Refuge in Utah where she realized her passion for birds (particularly shorebirds) and traveling. This launched her career as a gypsy-biologist, where research opportunities took her to various states and countries. After working with Snowy Plovers in Florida with FWC, continued work with this species took her to graduate school at the University of Florida, where she completed her master's degree in wildlife ecology and conservation. She is not sure where she will head next, but would like to continue to work with shorebird conservation and associated coastal habitats.