Assessing habitat selection, reproductive performance, and the affects of anthropogenic disturbance of the Snowy Plover (*Charadrius alexandrinus*) using spatial and temporal scale influences

Raya Ann Pruner
University of Florida, Department of Wildlife Ecology and Conservation

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

Habitat Selection: Selection of breeding habitat is an important decision for many species (Rosenzweig 1987). However, traditional studies have primarily focused on game species and temperate forest habitats. In general, 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 (Block and Brennan 1993, Thomas and Taylor 1990, 2006) and can be measured through comparisons of use of resources and habitat relative to their availability (Manly et al. 2002, Thomas and Taylor 1990, 2006). 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 (Colwell et al. 2005, Garshelis 2000).

Arguably, food availability is the single most important determinant for patterns of selection and species occurrences in natural communities (Granadeiro et al. 2004, Frederick et al. 1996) due to energy requirements associated with both reproduction and survival (Schekkerman and Visser 2001). Other possible determinants include predator avoidance, competition, human disturbance, and habitat alteration (Page et al. 1995). Recently, the effects of anthropogenic alteration, wide-scale habitat loss, and rising sea-levels on the habitat selection process are of interest to researchers and public land managers, because such effects can have dramatic consequences for population dynamics. Such issues 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). Furthermore, predicting the effects of local habitat alteration and loss on a broad landscape-level requires an understanding of how habitat selection affects local reproduction, survival, and dispersal (Cohen et al. 2006). 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 are beginning to receive 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 (Lafferty 2001a, 2001b, Burger 2000, Chase and Gore 1989). 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 60km of the coast (Roberts and Hawkins 1999), leading to increases in direct pressures to coastal environments and coastal-dependent species (Burger 2000). The largest 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 to shorebirds: The selection of breeding habitat may be influenced by a combination of factors: human recreational activities, predation of eggs and chicks, food availability, and natural disturbance associated with weather (Colwell et al. 2005). Contrary to management views on the necessity of anthropogenic beach stabilization, coastal-dependent species, such as shorebirds (*Charadriiformes*), are well adapted to dynamic environments (Haig and Elliot-Smith 2004, Gore 1996). However, they must find suitable habitat for multiple reproductive behaviors within a single landscape and must select habitats that provide adequate nesting, brood-rearing, refuge, and roosting (Conway et al. 2005, Haig et al. 1998). Energy requirements and related movement needs for self-feeding precocial young are poorly understood. Yet, it is known that they must have a reliable food supply for successful development because the burden of collecting necessary food is shifted to the chick (Schekkerman and Visser 2001). However, brood success is difficult to study because nidifugous chicks typically leave nesting areas only a few hours after hatching. In fact, broods have been observed at brood-foraging areas several kilometers away from original nesting sites (per. Ob). Brood-foraging areas are defined as low-wave energy moist sediment habitat. Due to this behavior, brood-rearing requirements within the landscape are largely unknown and ignored in management plans.

Additionally, alteration and loss of habitat has intensified the spatial overlap between coastal birds and humans (Weston and Elgar 2007). An increase in human-bird contact alters use-patterns within the landscape by excluding shorebirds from potential feeding areas (Stillman 2003, Gill et al. 2001). Consequently, recreational activities are a central cause of population declines in many species listed as federally threatened or endangered (Czech et al. 2000). Tourism has resulted in increased recreational pressures on coastal habitats and has contributed to global declines in coastal-dependent species, particularly shorebirds (Gill et al. 2001, Yasue and Dearden 2006, Burger 2000, Lord et al. 2001, Ruhlen et al. 2003). 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 2006). Interests in the effects of human disturbance has increased in recent years (Gill et al. 2001, Yasue and Dearden 2006, Burger 2000, Lord et al. 2001, Ruhlen et al. 2003, Lafferty et al. 2006, McCrary and Pierson 2000) and have produced an array of contrasting conclusions.

Shorebirds respond to anthropogenic disturbance in various ways (watching, walking, or flushing), depending on the proximity and type of human activity (walking, running, dog exercising, etc) (Burger and Gochfeld 1991, Burger 1994). These reactions result in a reduction in foraging efficiency and possible abandonment of foraging areas (McCrary and Pierson 2000, Lafferty 2001a, 2001b, Burger and Gochfeld 1991, Burger 1994). The change in shorebird behavior is assumed to be due to the perceived predation threat of humans (Yasue 2006). However some researchers consider anthropogenic disturbance to be a poor predictor of shorebird presence and/or density (Finn et al. 2007, Yasue 2006, Gill et al. 2001). Research on coastal invertebrates suggests that it is possible for prey abundance to be high enough to compensate for negative human impacts (Finn et al. 2007, Smith and Faillace 2006, Gill et al. 2001). These data suggest that anthropogenic alteration of coastal habitat structure, which in turn may impact prey abundance, may affect shorebird distribution more extensively than anthropogenic disturbance alone.

Predation: Ground-nesting shorebirds birds such as the snowy plover (*Charadrius alexandrinus*) are generally vulnerable to, and their breeding habitats are greatly influenced by, predators in coastal habitats (Page et al. 1983). However, increases in recreational pressures and unfavorable management practices applied on public beaches have rendered many unsuitable as nesting habitat (Gore 1996) resulting in habitat loss. Habitat loss has subsequently led to increases in snowy plover nest density at the few remaining breeding sites (Himes et al. 2007). The maintenance of low nesting density is an important anti-predator adaptation (Page et al. 1983) for solitary ground-nesting species. Solitary nesters' depend upon their cryptic color patterns and anti-predator displays to camouflage their presence from predators (Page et al. 1995). Increases in nesting density in response to loss of habitat may contribute to population declines due to increased predation pressure, particularly by scavengers attracted to garbage (Lafferty 2001a).

The main predators observed in previous Florida surveys, based on tracks, included canid species, raccoons, and ghost crabs (Himes et al. 2007). It is unclear if ghost crabs are a source of predation. Despite documented ghost crab depredation on piping plover eggs (Watts and Bradshaw 1995) and chicks (Loegering et al. 1995), there is no strong correlation between low recruitment and high ghost crab abundance (Wolcott and Wolcott 1999). However, in the most recent FWC survey, crab burrows were frequently observed within the vicinity of snowy plover nests during the expected hatch dates (Himes et al. 2007). Ghost crabs were also observed excavating burrows from previously active

snowy plover nests, presumably depredating the eggs in the process. Ghost crabs typically excavate burrows immediately adjacent to potential food, which provides security for extended scavenging (Wolcott and Wolcott 1999). Ghost crabs have also been observed directly predating upon snowy plover chicks (B. Eells, pers. comm.). In addition, fish crows and laughing gulls were observed taking snowy plover eggs (pers. Obs.) and chicks (B. Eells pers. comm.).

Chronically low reproductive rates have been identified as a major cause for population decline in snowy plovers (Colwell et al. 2005). Thus, it is essential to determine the reproductive success, and predation rates, as well as identify the types of predators that might be influencing nest success and recruitment at various sites. Habitat restoration or controlling recreational disturbance may be inconsequential if fledging success remains low (Himes et al. 2007).

Snowy plover (*Charadrius alexandrinus tenuirostris*): The snowy plover is one of the most threatened bird species in the U.S. (Gorman and Haig 2002, Funk et al. 2007) due to its patchy distribution and wide-spread loss of habitat. Although controversial (Funk et al. 2007, Gorman 2002), at least 6 morphologically distinct subspecies are recognized (O'Brien et al. 2006), 2 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). This study is primarily concerned with Cuban snowy plovers distributed along the Florida Gulf Coast. The Florida Fish and Wildlife Conservation Commission (FWC) conducted 3 state-wide surveys, 1989 (Chase and Gore), 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 the Southwest (Himes et al. 2007).

The snowy plover population in Florida is particularly vulnerable since they are restricted to barrier islands and a few coastal mainland beaches along the Gulf Coast, and it presumably functions as a demographically independent 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 potential 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 the tourism season (Himes et al. 2007, Lamonte et al. 2006, Chase and Gore 1989). 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. However, because of the lack of historic data on the Florida population the demographic response to either habitat loss or alteration has not been documented. Nevertheless, the increasing human population and loss of coastal habitat to development and disturbance has resulted in declines of available habitat and consequently, in the population of snowy plovers (Gore 1996).

Although many studies have demonstrated population declines due to predation (Page et al. 1995), others have demonstrated changes in habitat use and breeding success as a result of human disturbance (Yasue and Dearden 2006, Ruhlen et al. 2003, Burger and Gochfeld 1991). However, most studies have examined disturbance in isolation from ecological factors (Yasue and Dearden 2006). Thus, there is a need to incorporate variables related to habitat use and selection, human disturbance, alteration of habitats, environmental factors, and potential predation (Yasue 2005, Stillman and Goss-Custard 2002, Gill et al. 2001b). This allows for more accurate assessment of human disturbance and ecological factors that may affect breeding success (Yasue 2005, Frid and Dill 2002). In addition many broad-scale studies have demonstrated that snowy plovers breed on sandy beaches with open bare ground (Chase and Gore 1989, Lamonte et al. 2006, Hood 2006) however, habitat requirements for snowy plover broods are less understood. Given the high energy demands and high mortality of most shorebird chicks to either starvation or exposure (Pearce-Higgens and Yalden 2003), it is likely that habitat selection and diet are critical for their survival.

This study specifically focuses on identifying potential detrimental impacts to the snowy plover population with the goal of preserving access to high quality brood-rearing habitat to ensure reproductive rates that will sustain the local population. 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.

Methods

Study Area: Research was conducted at six sites located contiguously in Franklin, Gulf and Bay Counties, in the panhandle of Florida. Sites included are Shell Island (SH-D) (5.2km; St. Andrews State Park), Shell Island (SH-T), Crooked Island East (CIE), West (CIW), & Buck Beach (BB) (21.5km; Tyndall Air Force Base), Bonfire Beach (BF) and Windmark (WM) (5.2km; The St. Joe Company), St. Joseph's State Park (SJ) (13km), and St. Vincent NWR (SV) (12.5km). All sites except Windmark and Buck Beach are barrier Islands along the Gulf Coast. These two sites are the only mainland sites in the area supporting snowy plover breeding. For the habitat selection data, we chose these sites due to variation in habitat physical attributes (e.g., shell debris, level of dunes, presence of wash-over areas, etc.), variation in human disturbance background levels, variation in predator presence and because these sites represent a large proportion of the Florida snowy plover population (41%; Himes et al. 2007).

We conducted nest and brood surveys every 3-5 days between February and August of 2008 and 2009. These dates correlate with the range in breeding documented in Florida during previous studies (Himes et al. 2007). We searched for nests systematically in suitable breeding habitat areas. We used a leap-frog method for nest searching, with one person walking the nesting habitat and a second person using an atv on the shoreline moving ahead up the beach a given distance. Once snowy plovers are located, we determine if plovers were exhibiting breeding behavior. For nesting pairs (birds actively defending scrapes with eggs), we watched from a distance for the individual to return to their nest or located nest by following snowy plover tracks. For families (adults with unfledged chicks) we either watched for family behavior and/or for resumption of normal behavior (e.g., brooding of chicks). For territorial pairs, (a pair of birds defending an area, but without nests containing eggs), we searched for nest scrapes and document them for future investigation. We conducted all observations with 10 x 42 binoculars or a spotting scope.

As nests were located, we recorded location using handheld GPS unit. If nests were located with a full clutch, we used egg floatation to detect embryo mortality and to estimate lay and hatch dates (see Hood 2007 for chart). For this study, we used the reported incubation length of 25-27 days for snowy plovers nesting in Florida (Chase and Gore 1989). Using this incubation range, Hood (2007) determined egg floatation to be accurate within 1-2 days for other Gulf Coast populations (i.e. Texas). Snowy plovers do not begin incubating until the 3rd egg in the clutch is laid (Page et al. 1995). For this reason, estimating hatch-date via floatation is only possible after a full clutch is laid. Snowy plovers typically take 4 days to lay complete clutch (Warriner et al. 1986), so for incomplete clutches, we estimated hatch-day by adding potential lay-days. Nests were monitored until either cessation (hatch or fail). In all cases fate is known. We verified hatching by the presence of chicks, brood tracks at the nest, or by family behavior from adults. We determined depredation by presence of predator tracks at nest or by nest disappearing to early in incubation to have hatched.

For nests that hatched, adults and chicks were individually marked on hatched day with UV resistant darvic color bands. Parents were caught using a modified funnel trap and a chick coral (around chicks or eggs) either late in incubation or shortly after hatching (see Gratto-Trevor 2004). We continued monitoring chicks (concurrent with nest observations) every 3-5 days until fledge (28 days post-hatch; Warriner et al. 1986). We recorded the location of broods with GPS units to determine the distance traveled from nests. We also classified the brood-rearing habitat used by each brood (i.e. ephemeral pools, beach fronts, or bay tidal flats).

We created random points for habitat selection models through ArcGIS 9.2 by creating polygons of potential nesting habitat, based on aerial photographs and personal experience. Within potential nesting habitat, we overlayed a grid system (100m x 100m) and ran a random point generator (Hawth's tools) to select points within each grid. We randomly selected 50% of these to be used in our study.

At each nest and random point location we collected measurements at 3 spatial scales, microhabitat ($1m^2$ radius), macrhabitat (100m), and landscape level (500m) to test 4 *a priori* hypotheses. *Hypothesis 1:* breeding habitat is determined by habitat physical attributes *Hypothesis 2:* breeding habitat is determined by human activity, *Hypothesis 3:* breeding habitat is determined by proximity to brood-rearing habitat, and *Hypothesis 4:* breeding habitat is determined by predator activity.

Hypothesis 1: Habitat physical attributes

At the microhabitat scale, we quantified the percent cover of each habitat type (i.e., vegetation, bare sand, shell debris, organic debris, and other) within the $1m^2$ radius. At the macrohabitat scale we use a distance to object design,

measuring: distance to vegetation, type of vegetation, primary dune, height of dune, distance to nearest conspicuous object, within a $100m^2$ radius.

Hypothesis 2: Human activity

At the macrohabitat scale we use a distance to object design, measuring: presence/absence of beach access points, type of beach access point (e.g., boat access, boardwalk, etc.), distance to nearest human foot print, and presence/absence of symbolic fencing within a $100m^2$ radius. To investigate the spatial variation in human disturbance potentially affecting nest site selection and nest/brood success, we quantified human presence by footprints. At the landscape level we systematically sampled human activity. We set up strip transects by raking 50 m long x 4 m wide smooth sand transects running perpendicular from the shoreline to the primary dune line. Transects were set-up over the weekend and observed human tracks were counted. To investigate temporal variation, we conducted index transects twice during the breeding seasons.

Hypothesis 3: Brood-rearing habitat

At the macrohabitat scale we use a distance to object design, measuring: the distance from the nest to the nearest body of water, type of water body (i.e., wash-over area, ephemeral pond, gulf shoreline, bay shoreline, etc) within a $100m^2$ radius. At the landscape we systematically sampled prey availability. To investigate annual variation in food availability we sampled for epifaunal (surface-dwelling) invertebrates during July and August 2008 and 2009. We sampled invertebrates utilizing pitfall traps and paint stirring sticks coated with Tanglefoot (The Tanglefoot Company). We systematically sampled for invertebrate by selecting a random point every 500m of linear beach habitat. We set up intertidal strip transects through random points running perpendicular from the shoreline to the vegetation line (Figure 3). We arranged 5 sample arrays along a straight line between the high and low water marks perpendicular to the shoreline. The first array was centered on the most recent wrack-line, the second array was halfway between the recent wrack-line and the highest wrack-line. The third array was centered on the highest wrack-line. The forth array was halfway between the highest wrack-line and the vegetation line. The fifth array was directly in front of the vegetation line.

An array consist of four pitfall traps made of clear plastic (diameter 11cm, depth 8cm) placed 2m apart in a 2m x 2m plot and 8 tangle foot sticks, 2 at each corner (1 vertical and 1 horizontal). We placed each pitfall trap flush with the substrate and fill each with 1cm of propylene glycol and H20. We left arrays open for 1 hour beginning 1 hour after low tide. After 1 hour, trap contents were collected, filtered with a sieve, and invertebrates were counted. These methods of prey sampling are appropriate because snowy plovers do not probe beneath the surface (Yasue 2006). Snowy plovers employ a 'picking' feeding method using a 'run-and-pause' style based upon visual cues (Message and Taylor 2005). To verify that invertebrate sampling accurately captures prey availability, we opportunistically monitored foraging by adults and broods through observation to identify prey items captured.

Hypothesis 4: Predator Activity

At the macrohabitat scale we use a distance to object design, measuring: presence/absence of forest edge, nearest ghost crab burrow within a $100m^2$ radius. Tracking animals by following footprints in substrates such as sand is probably the oldest known and most efficient method of identifying mammal's presence in an area (Bider 1968, Silveira et al. 2003). At the landscape level we systematically sampled predator activity. We set up strip transects by raking 50 m long x 4 m wide smooth sand transects running perpendicular from the shoreline to the primary dune line. Transects were set-up over the weekend and observed predator tracks were counted by type and ghost crab burrows were also counted. To investigate temporal variation, we conducted index transects twice during the breeding seasons.

Competition

Because we were also interested in the potential negative effects of increased nest densities, we used nearest neighbor distances as a measurement of potential competition from neighboring nesters. Using Hawth's Tools nearest neighbor extension in ArcGIS 9.2, we calculated the distance to nearest snowy plover nest to account for intraspecific competition and we calculated the distance to the nearest Wilson's plover nest to account for interspecific competition.

Brood-rearing habitat use

In addition to measuring nesting habitat use and availability, we quantified actual brood-rearing habitat use through an instantaneous sampling design. This data allowed us to determine whether snowy plovers select nesting habitat based

on predetermined knowledge of brood-rearing habitat. We collected all data during brood monitoring phases of the study. We recorded each observed brood location with a GPS unit and we record the type of brood-rearing habitat used (i.e., ephemeral pool, beach front, bay tidal flat). We calculated the distance traveled by brood from nesting area to brood-rearing area. For broods with multiple observations, we used the average distance traveled.

Statistical Anlaysis

Habitat Selection

To identify factors influencing territory selection, we compared micro and macrohabitat characteristics of actual nests sites to control (randomly-generated) areas. For each of the *a priori* habitat selection hypothesis (i.e., physical attributes, food abundance, human and predator presence), we used logistic regression models (Broders and Forbes 2004). We employed this method because the dependent variable (y) was categorical (i.e., presence or absence) and the independent (x) was mixed categorical and continuous data (e.g., distance from water, type of water body, etc.). We also include covariates such as date and temperature as independent variables.

Factors affecting Reproductive Performance

To estimate nest and brood success, we used a logistic-exposure method that accounts for variation in exposure days among nests (Shaffer 2004). Using the linear logistic exposure model, we modeled reproductive performance as a function of habitat selection factors (i.e., habitat metrics, prey availability, and human and predator activity) using both categorical and continuous variables. Models also included nearest neighbor distance to account for spatial dependence. We used Akaike's Information criterion to rank candidate models (Burnham and Anderson 2002). Using this method, we identified factors that influenced the hatch and brood success rates. Additionally, the logistic-exposure approach allowed for analyzing the effects of time-specific variables (Shaffer 2004). In this case, we allowed for testing temporal variation between study years and by month for correlation with the tourism season (changes in anthropogenic disturbance levels).

Summary Results

Nesting Activity

During the 2008-9 breeding seasons, we located 473 nests. Specifically, we located 190 and 283 during 2008 and 2009, respectively (see Fig. 1 for nest distribution across sites). Nests were initiated from March until August, with the peak in initiation occurring in May (Fig. 2). Nest Chronology was similar between seasons. However, during 2009, instead of having one peak in nest initiation, nests were initiated at a consistent rate from April through June.

Approximately the same number of nests hatched during both seasons, 101 in 2008 and 106 in 2009. However, the apparent hatch rates differed due to the total breeding effort (Fig. 3). 101 nests or 53.2% of 190 nests hatched successfully in 2008. 106 nests or 37.5% of 283 nests hatched successfully in 2009. We observed a combined hatch rate of 43.7%.

During both seasons hatch rates differed by site, with Windmark Beach experiencing the lowest hatch rate (0%) and Bonfire Beach and St. Vincent NWR experiencing the highest hatch rates during both seasons (Fig. 4). Hatch rates differed significantly across all sites between the two seasons ($\chi 2=3.8864$, df= 1, p-value= < 0.05) (Fig. 3). The primary cause for nest failure was predation during both seasons. In fact, approximately 88% of all nests failed during both seasons due to predation. The difference in hatch rates between seasons was most likely due to a change in predator numbers. The results of our predator index counts indicated a significant increase in predator numbers during 2009 when compared to 2008 (t= 2.348, df=123, p-value= <0.05). We observed increases in both ghost crab and canid counts at all sites during the 2009 breeding season. Similarly, we observed and increase in the number of nests depredated by both ghost crabs and canids in 2009 (Fig. 5 & 6).

We collected data at each nest at 3 spatial scales (microhabitat, macrohabitat, and landscape) to contrast 4 *a priori* hypotheses that had a potential to influence nest-site selection, and nest survival. Our 4 hypothesis of interest were, the influence of human activity, predator activity, prey availability, and habitat features on selection and survival during both nest and brood stages. Selection and survival were in fact influenced by additive effects from all 4 *a priori* hypotheses. Plovers selected beaches based on the presence of symbolic fencing, absence of a tree line within 200m,

distance to ghost crab burrows, distance to conspicuous objects and the distance and type of brood-foraging habitat. The likelihood of hatching nests was influenced by year, the presence of symbolic fencing, distance to ghost crab burrow, distance to Wilson's plover nest, and the distance to the dune (*for more detail, see Pruner Thesis chapter 1*).

During 2009 we located a total of 63 nests in which 1st year birds (those that fledged during the 2008 season) laid. However, the hatch and fledge rates for 1st year birds were significantly lower than over all plover age classes ($\chi^2=$ 3.79, df= 1, p-value= <0.05). The apparent hatch rate for 1st year birds was 26.9%. Additionally, of those that were able to successfully hatch a nest, only one was not paired with an older adult. Only three 1st year birds were able to successfully fledge chicks, with an apparent fledge rate of 17.6%, all with an older adult mate. In fact, if we remove the nests of all 1st year birds from the overall nests and just calculate the hatch rate for known older adults, the hatch rate is 46.5%. This is 20% greater than 1st year birds.

Brood Activity

During our study, we marked a total of 507 individuals, 140 were banded as adults, and 367 were banded as chicks (see table 1 for site distributions). A majority of the adults were marked during the 2008 breeding season, 118 in comparison to 22 adults in 2009. We used the presence and activities of marked adults to aid in the determination of brood fates. Through band re-sights of both individual chicks and adults we determined that 90 and 55 chicks fledged during 2008 and 2009, respectively. Based on the total chicks marked during both seasons, this indicates a 45.5% fledge rate in 2008 and a 32.7% fledge rate in 2009. At the brood level, we determined 64 (63.4%) and 50 (48.1%) nests to have fledged at least 1 chick during 2008 and 2009, respectively (see Fig. 7 for apparent hatch rates across sites). Although there was a significant difference in the hatch rates between season, the overall number of hatched nests to fledge at least 1 chicks between season was not significant ($\chi^2=2.368$, df= 1, p-value= > 0.10) despite the lower rates observed in 2009.

Site	SH-D	SH-T	CIW	BB	CIE	BF	WM	SJ	SV	Total
Adults	23	4	29	0	18	8	0	35	23	140
Chicks	46	14	76	6	53	35	0	87	50	367
Total	69	18	105	6	71	43	0	126	73	507

Table 1. Number of individuals banded during project by site.

While monitoring brood activity, we calculated the distance broods traveled from the nest territory to brood foraging areas. The average distance broods traveled was 729 m, with a maximum distance traveled of 5.3 km. This is in contrast to studies with unmarked individuals that typically assume a defended territory of 100 to 200m around the nest location in determining productivity (Himes et al. 2007). We defined 3 basic brood foraging habitat types for this study (ephemeral pools, beach front, and bay tidal flats). We calculated the proportion of each habitat type in our study system and during brood observations we identified the habitat type used by each individual brood. Based on this information we calculated a standardized selection index (see Manley et al. 2002). We used a Chi-Square contingency table of observed to expected to test the hypothesis of no selection between brood foraging habitats. Our results indicated the presence of selection between habitats ($\chi^2 =110.443$, df= 2, p-value= < 0.00001). By using Bonferroni adjusted confidence intervals to the selection index, we calculated which habitats were selected for. Ephemeral habitats were selected for brood foraging, beach front habitats were avoided, and there was no preference for bay tidal flats.

We contrasted 4 *a priori* hypotheses that had a potential to influence brood survival. Our 4 hypothesis of interest were, the influence of human activity, predator activity, prey availability, and habitat features on brood survival. The likelihood of fledging a clutch was influenced by year, the percent debris cover around the immediate nest, age of chick, and the type of brood-foraging habitat used. Broods that used ephemeral pools were more likely to fledge at least one chick compared to broods that foraged at bay flats or at the gulf front (*for more detail see Pruner Thesis chapter 2*).

Band Re-sights

Between the two breeding season, based on band re-sights, we had a return rate of ~90% for adults returning to the site in which they previously bred and 45.6% for 1st year birds returning to their natal sites (defined as philopatry). These numbers are similar to those observed during long term studies with snowy plovers. We observed no difference by gender with 20 philopatric males and 21 females. An additional 4 1st year birds were confirmed breeding elsewhere at Eglin AFB.

During the winter months of both seasons we received band resights from volunteers, biologist, land managers, and birders. The majority of resights were at or near our research sites indicating a tendency for birds to remain as residents during the winter months. However, one individual was observed 293 km to the east at Horn Island, MS. Three others were observed at Dauphin Island, AL. An adult was also observed dispersing 540 km to the south to Sanibel Island, FL. Many others have been observed at other locations in the Florida peninsula at sites such as Fort DeSoto, Stump Pass SP, Honeymoon Island, and Longboat Key.

Discussion

Nesting Activity

Snowy plovers exhibited annual variation in the timing of nesting. Although the initial peak in nesting was similar between seasons, the consistent rate of initiation from April through June in 2009 was most likely a result of the high nest failure rate and the subsequent laying of replacement clutches. This pattern is consistent with the increase in the number of nests across all sites in 2009 and the significant difference in hatch rates between the two seasons. This indicates that the increase in nests located during 2009 was a result of an increase in replacement clutches in response to high predation rates and not the slight increase in the number of breeding pairs between these two seasons.

Snowy plovers also exhibited annual variation in nest survival, a pattern similar to other areas where the species' breeding biology has been studied (values range from 13% to 72%; see Lauten et al. 2007, Warriner et al. 1986), although this pattern was only based on two years of data. The implications of this short term pattern are unclear, but this study does provide important baseline data on the snowy plover nesting ecology for the Florida population.

One potential reason for the variation in nest survival and the related timing of nesting is the increase in predator numbers between the two seasons. The increase in canid numbers may be related to the lack of predator control during the 2009 season at most of our research sites. However, the increase in ghost crab density needs further exploration. Ghost crab densities are however tightly correlated with both temperature and moisture (Wolcott 1978). The environmental conditions during 2009 may have been favorable to ghost crabs.

Nest selection and survival patterns revealed in this study indicate an influence by several factors working in concert. Nest-site selection and nest survival were influenced by human and predator activity, prey availability and habitat features. The two factors that influenced both selection and survival were the distance to the nearest ghost crab burrow and the presence of symbolic fencing. The influence of ghost crabs on nest-site selection is likely due to the perceived threat to adults. Adult plovers are often observed with leg wounds from ghost crabs (pers. Obs.). The influence of symbolic fencing on nest-site selection is understandable as it eliminates the presence of human disturbance. However, the influence on survival is less clear because the failure of nests without symbolic fencing was primarily due to depredation by ghost crabs. This suggests a potential indirect predation effect from human disturbance. Unlike other species of crabs, ghost crabs are not scavengers. In fact, they prefer live prey and are attracted to prey primarily by movement (Wolcott 1978). This behavior may explain the increase in predation with the absence of symbolic fencing. Because human disturbance can cause plovers to flush from the nest more frequently and for longer periods of time (Weston and Elgar 2007, Baudains and Lloyd 2007) ghost crabs may be responding to such movement corresponding to the increase in predation rates.

Our results also indicate the potential for experience to influence nest survival. However, this was not included in our models because we did not have age data for the 2008 season. However, the significant difference in hatch rates between 1st year birds and older adults suggest the importance of experience in nest survival. Taking this into account, the variation in nest survival between seasons should be viewed cautiously as a successful season may negatively

influence survival the following year due to the increased number of inexperienced 1st year birds in the breeding population.

Brood Activity

Snowy plovers exhibited annual variation in brood survival, comparable to the range of values identified in other longer term studies in other breeding populations (11% to 54%; Lauten et al. 2007). These are the first wide-scale values indicating brood survival for the snowy plover population in Florida. Therefore, it is unclear how these values compare to the average for this particular population. However, although not significant, we did observed a decrease in brood survival during 2009 concurrent with observed increases in predator densities and decreases in nest survival. The primary cause for chick failure is predation and the probability of predation is often linked to chick age (Warriner et al. 1986, Sandercock et al. 2005, Colwell et al. 2007).

Brood survival was influenced by additive factors from two of our *a priori* hypotheses, brood-rearing habitat and habitat features. Specifically, brood survival was influenced by percent debris around the immediate nest site and the type of brood rearing habitat used in addition to brood age and year. We included year in the survival analyses to account for annual variation that is a common finding in birds in general. Observing differences between years is often assumed to be related to changes in weather or predator communities. For this study we did observe a significant difference in the predator densities between years. However, we measured predator densities at the landscape level (500m). This may have been too coarse a measurement to capture the relationship to brood survival. Additionally, broods are mobile and capable of travelling long distances and therefore may be exposed to varying predator densities.

Age related survival has been documented in other studies. For example, Colwell et al. (2007) found age-dependent survival of snowy plover chicks to parallel trends of increasing development, thermal independence from adults, and capability of evading predators. Therefore, it is not surprising to observe these patterns in our system where changes in the predator community appear to impact both nest and brood survival. The tendency for chicks < 1 week to remain motionless when threatened makes them more vulnerable to ghost crab predation.

In light of the low brood survival during the first week, it is not surprising to see survival positively influenced by the percent debris around the immediate nest site. Many studies have documented debris around nest sites as a camouflage technique to protect the eggs. This is the first study that we know of that has linked debris as a positive influence on brood survival. Debris around the immediate nest site likely does provide camouflage from predators, both avian and terrestrial. In fact, because ghost crabs respond to movement, they must taste objects to find motionless prey (Wolcott and Wolcott 1999). Therefore, a greater percentage of debris around the nest may confuse ghost crabs and decrease the probability of predation. Additionally, with high ambient temperature during the summer months, debris may provide shade during the early stages when chicks lack thermal independence.

Snowy plover broods selected for ephemeral pools beyond their availability compared to all brood-foraging habitat types in the survey areas. Additionally, brood-foraging habitat type influenced brood survival. Broods that foraged at ephemeral pools had the highest survival when compared to broods that foraged at either beach front habitats or bay tidal flats. In fact, broods were travelling long distances from nesting sites due to the location of this preferred brood-foraging habitat. These results highlight the importance of this high-prey, low energy habitat type. It is surprising that snowy plover broods showed no preference for bay tidal flats, another high-prey habitat. However, bay tidal flats are often highly open and exposed to predators. We often observed a transition to bay tidal flats as broods fledged. Beach front habitats not only had the lowest level of available prey, but often had the highest levels of both predator and human densities. Therefore, it is not surprising that broods avoided and broods had the lowest level of survival at beach front habitats.

The use of symbolic fencing, although it positively influenced both nest-site selection and survival, had no influence on brood survival. This is likely due to the mobility of broods. This also highlights the potential for improved brood survival rates with the placement of symbolic fencing around brood-rearing areas such as ephemeral pools. Posting of ephemeral pools will not only improve brood survival, but will additionally aid in nest survival. Nest-site selection was positively influenced by the presence of ephemeral pools and therefore placing fencing around this habitat type will likely improve the nesting habitat as well and decrease the distance travelled by individual broods.

Band Re-sights

The philopatric rate observed was comparable to values observed during long term studies with snowy plovers in other regions. For example, Colwell et al. (2007b) documented a 31.5% philopatric rate over a 5 year period. Lauten et al. (2007) documented return rates ranging from 29% to 64% over an 18 year period, with an average of 45%. Likewise, observing no difference in philopatric rates between males and females was consistent with other studies. Colwell et al. (2007b) also noted no difference in patterns of natal dispersal between males and females.

Ongoing efforts to get winter re-sights to compare breeding versus winter dispersal as well as ascertain potential differences in feeding habitat during these two seasons continues. This data will be analyzed at a later date.

Recommendations

Signing of Restricted Areas

Symbolic fencing improved both nest-site selection and hatch rates. Therefore, signing and roping should continue to be implemented to inform the public of plover nesting habitat and direct the public away from the nesting areas. Storms in the season often make posting areas a challenge, but it is important to have signs in place beginning on 1 March. Maintenance of signs is important to keep violations to a minimum. To maximize the effectiveness of signs and ropes each site should continue to be evaluated and ways to improve the signing and ropes should be considered. Roped nesting areas act as a safe refuge from recreational activity on the beach, but plover broods do not stay within the confines of the nesting area and broods are often found foraging at ephemeral pools, bay tidal flats, the wrackline or on wet sand, particularly in the morning before beach activity increases. Signing of foraging areas should be considered alongside the current posting of nesting areas.

Predator Control
The cause for nest failure at all sites was primarily due to depredation. This research also documented a significant difference between hatch rates during 2008 and 2009 concurrent with a significant increase in predator densities. Therefore, predator management should be maintained at all sites. There is also a need to explore ways of better understanding the activity patterns and population levels of predators, particularly ghost crabs and coyotes.

Nest Monitoring
Snowy plovers should continue to me monitored during the breeding season until we have a better understanding of the annual variation in nest and brood success. Monitoring marked individuals will additionally allow for a more accurate calculation of the population size. Furthermore, the monitoring of plover population size and productivity will ensure that the Florida populations are maintained.

Winter Monitoring
Monitoring during the winter season should continue to better understand the winter habitat requirements for this species and other shorebirds that utilize these sites during the winter season. Additionally, monitoring marked individuals during the winter allows for determination of dispersal distances and whether the Florida snowy plover population in a resident or migratory population.

Literature Cited

Bennett J, Wallace GE. 2001. An Annotated Bibliography for the Snowy Plover (*Charadrius alexandrinus*) in Florida. Tallahassee (FL): Florida Fish and Wildlife Conservation Commission.

Bider JR. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecological Monographs 38(4):269-308.

Brown AC, McLachlan A. 2002. Sany shore ecosystems and the threats facing them: some predictions for the year 2025. Environmental Conservation 29(1):62-77.

Burger J. 1986. The effects of human activity on shorebirds in two coastal bays in Northeastern United States. Environmental Conservation 13(2):123-130.

Burger J. 1994. The effect of human disturbance on foraging behavior and habitat use in piping plover (Charadrius melodus). Estuaries 17(3):695-701.

Burger J. 2000. Landscapes, tourism, and conservation. The Science of the Total Environment 249:39-49.

Burger J, Gochfeld M. 1991. Human activity influence and diurnal and nocturnal foraging of sanderlings (Calidris alba). Condor 93:259-265.

Chase CA III. 1991. Population status of the snowy plover breeding and wintering on Eglin Air Force Base [thesis]. Tallahassee (FL): Dept. of Biological Sciences, Florida State University.

Chase CA III, Gore JA. 1989. Snowy Plover breeding distribution. Tallahassee (FL): Florida Game and Fresh Water Fish Commission. Final Performance Report.

Czech B, Krausman PR, Devers PK. 2000. Economic associations among causes of species endangerment in the United States. BioScience 50:593-601.

Cohen JB, Fraser JD, Catlin DH. 2006. Survival and site fidelity of piping plovers on Long Island, New York. Journal of Field Ornithology 77(4):409-417.

Colwell MA, Millett CB, Meyer JJ, Hall JN, Hurley SJ, McAllister SE, Transou AN, LeValley RR. 2005. Snowy Plover reproductive success in beach and river habitats. Journal of Field Ornithology 76(4):373-382.

Colwell MA, Hurley SJ, Hall JN, Dinsmore SJ. 2007a. Age-related survival and behavior of snowy plover chicks. The Condor 109:638-647.

Colwell MA, McAllister SE, Millett CB, Transou AN, Mullin SM, Nelson ZJ, Wilson CA, LeValley RR. 2007b. Philopatry and natal dispersal of the western snowy plover. The Wilson's Journal of Ornithology 119(3):378-385.

Conway WC, Smith LM, Ray JD. 2005. Shorebird habitat use and nest-site selection in the Playa Lakes region. Journal of Wildlife Management 69(1):174-184.

Fahrig L, Merriam G. 1994. Conservation of fragmented populations. Conservation Biology 66:1762-1768.

Finkl CW. 1996. What might happen to America's shoreline if artificial beach replenishment is curtailed: a prognosis for southeastern Florida and other sandy regions along regressive coasts. Journal of Coastal Research 12:iii-ix.

Finn PG, Catterall CP, Driscoll PV. 2007. Determinants of preferred intertidal feeding habitat for Eastern curlew: A study at two spatial scales. Austral Ecology 32:131-144.

Frederick PC, Bildstein KL, Fleury B, Ogden J. 1996. Conservation of large, nomadic populations of white ibis (Eudocimus albus) in the United States. Conservation Biology 10(1):203-216.

Frid A, Dill A. 2002. Human-caused Disturbance Stimuli as a Form of Predation Risk. Conservation Ecology 6(1):11.

Funk WC, Mullins TD, Haig SM. 2007. Conservation genetics of snowy plovers. Conservation Genetics. In press.

Garshelis DL. 2000. Delusions in habitat evaluation: measuring use, selection, and importance In: L. Boitani and T. K. Fuller, editors. Research Techniques in Animal Ecology: Controversies and Consequences. New York (NY): Columbia University Press. p 111-164.

Gill JA, Norris K, Sutherland WJ. 2001. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. Journal of Applied Ecology 38:846-856.

Gore JA. 1996. Cuban Snowy Plover. In: Rodgers JA, Kale HW II, Smith HT, editors. Rare and Endangered Biota of Florida, Vol.5. Birds. Gainesville (FL): University of Florida Press. p 73-80.

Gorman LR. 2000. Population differentiation among Snowy Plovers (*Charadrius alexandrinus*) in North America [thesis]. Corvallis (OR): Oregon State University.

Gorman LR, Haig SM. 2002. Distribution and abundance of snowy plovers in eastern North America, the Caribbean, and the Bahamas. Journal of Field Ornithology 73(1):38-52.

Granadeiro JP, Andrade J, Palmeirim JM. 2004. Modelling the distribution of shorebirds in estuarine areas using generalized additive models. Journal of Sea Research 52:227-240.

Gratto-Trevor CL. 2004. The North American bander's manual for banding shorebirds (Charadriiformes, suborder Charadrii). North American Banding Council. Point Reyes (CA).

Groom MJ, Meffe GK, Carroll CR. 2005. Principles of Conservation Biology. Sunderland (MA): Sinauer Associates, Inc. 793 p.

Haig SM, Mehlman DW, Oring LW. 1998. Avian movement and wetland connectivity in landscape conservation. Conservation Biology 12(4):749-758.

Himes, JG, Douglass NJ, Pruner RA, Croft AM, Seckinger EM. 2007. Status and Distribution of the Snowy Plover in Florida. 2006 study final report. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

Hood SL. 2006. Nesting ecology of snowy and Wilson's plovers in the lower Laguna Madre region of Texas [thesis]. Mississippi State (MS): Mississippi State University. 78 p.

Kosztolanyi A, Szekely T, Cuthill IC. 2007. The function of habitat change during brood-rearing in the precocial Kentish plover *Charadrius alexandrinus*. Acta Ethol 10:73-79.

Jones J. 2001. Habitat selection studies in avian ecology: A critical review. The Auk 118(2):557-562.

Lafferty KD. 2001a. Birds at a Southern California beach: seasonality, habitat use and disturbance by human activity. Biodiversity and Conservation 10(2001):1949-1962.

Lafferty KD. 2001b. Disturbance to wintering western snowy plovers. Biological Conservation 101(2001):315-325.

Lafferty KD, Goodman D, Sandoval CP. 2006. Restoration of breeding by snowy plovers following protection from disturbance. Biodiversity and Conservation 15(2006):2217-2230.

Lamonte KM, Douglass NJ, Himes JG, Wallace GE. 2006. Status and Distribution of the Snowy Plover in Florida. Tallahassee (FL): Florida Fish and Wildlife Conservation Commission, 2002 final report.

Liley D and Sutherland WJ. 2007. Predicting the population consequences of human disturbance for ringed plovers *Charadrius hiaticula*: a game theory approach. Ibis 149(Suppl. 1):82-94.

Loegering JP, Fraser JD. 1995. Factors affecting piping plover chick survival in different brood-rearing habitats. The journal of Wildlife Management 59(4):646-655.

Loegering JP, Fraser JD, Loegering LL. 1995. Ghost crab preys on piping plover chick. Wilson Bulletin 107(4):768-769.

Lord AJ, Wass JR, Innes J. 1997. Effects of human activity on the behavior of northern New Zealand dotterel *Charadrius obsurus* aquilonius chicks. Biological Conservation 82:15-20.

Lord AJ, Waas JR, Innes J, Whittingham MJ. 2001. Effects of human approaches to nests of northern New Zealand dotterels. Biological Conservation 98(2001):233-240.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource Selection by Animals: statistical design and analysis for field studies. Norwell (MA): Klewer Academic Publishers. 219 p.

Martin TE. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656-670.

McCrary MD, Pierson MO. 2006. Influence of human activity on shorebird beach use in Ventura County, California. In: Lafferty, K. D., D. Goodman, and C. P. Sandoval. Restoration of breeding by snowy plovers following protection from disturbance. Biodiversity and Conservation 15(2006):2217-2230.

Mehl, K. R., K. L. Drake, G. W. Page, P. M. Sanzenbacher, S. M. Haig, and J. E. Thompson. 2003. Capture of breeding and wintering shorebirds with leg-hold noose mats. Journal of Field Ornithology 74: 401-405.

Nelson Z. 2007. Conspecific attraction in the breeding distribution of the Western Snowy Plover *(Charadrius alexandrinus nivosus)* [thesis]. Arcata (CA): Humboldt State University.

O'Brien M, Crossley C, Karlson K. 2006. The Shorebird Guide. Boston (MA): Houghton Mifflin Co.

Page GW, Stenzel LE, Winkler DW, Swarth CW. 1983. Spacing out at Mono Lake: breeding success, nest density, and predation in the Snowy Plover. The Auk 100:13-24.

Page GW, Warriner JS, Warriner JC, Paton PWC. 1995. Snowy plover *(Charadrius alexandrinus)*. In: Polle A, Gills F, editors. The Birds of North America,. Washington (DC): The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union. No. 154.

Paton, P. W. C. and T. C. Edwards. 1996. Factors affecting interannual movements of snowy plovers. The Auk 113(3):534-543.

Peterson CH, Bishop MJ, Johnson GA, D'Anna LM, Manning LM. 2006. Exploiting beach filling as an unaffordable experiment: Benthic intertidal impacts propagating upwards to shorebirds. Journal of Experimental Marine Biology and Ecology 338(2006):205-221.

Roberts CM, Hawkins JP. 1999. Extinction risk in the sea. Trends in Ecology and Evolution 14:241-246.

Robertson BA, Hutto RL. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87(5):1075-1085.

Rosenzweig M. 1981. A theory of habitat selection. Ecology 62(2):327-335.

Ruhlen TD, Abbott S, Stenzel LE, Page GW. 2003. Evidence that human disturbance reduces Snowy Plover chick survival. Journal of Field Ornithology 74(3):300-304.

Schekkerman H, Visser GH. 2001. Preflegling energy requirements in shorebirds: energetic implications of self-feeding precocial development. The Auk 118(4):944-957.

Shaffer TL. 2004. A unified approach to analysizing nest success. The Auk 121(2):526–540

Smith B, Faillace C. 2006. 2006 snowy plover conservation and research report for Sanibel Island, Florida. Sanibel (FL): Sanibel-Captiva Conservation Foundation.

Speybroeck J, Bonte D, Courtens W, Cheskiere T, Grootaert P, Maelfait JP, Mathys M, Provoost S, Sabbe K, Stienen EWM, VanLancker V, Vincx M, Degraer S. 2006. Beach nourishment: an ecologically sound coastal defence alternative? A review. Aquatic Conservation: marine and Freshwater Ecosystems 16:419-435.

Stillman R. 2003. Predicting wader mortality and body condition from optimal foraging behavior. Wader Study Group Bulletin 100:192-196.

Stillman RA, Gross-Custard JD. 2002. Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. Journal of Avian Biology 33:358-365.

Szekely T and Cuthill IC. 1999. Brood desertion in Kentish plover: the value of parental care. Behavioral Ecology 10(2):191-197.

Turner MG, Gardner RH, O'Neill. 2001. Landscape Ecology: In theory and practice, pattern and process. New York (NY): Springer Science. 401 p.

Thomas DL, Taylor EJ. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54(2):322-330.

Thomas DL, Taylor EJ. 2006. Study designs and tests for comparing resource use and availability I. The Journal of Wildlife Management 70(2):324-336.

Warriner JS, Warriner JC, Page GW, Stenzel LE. 1986. Mating system and reproductive success of a small population of polygamous snowy plovers. Wilson Bulletin 98(1):15-37.

Watts BD, Bradshaw DS. 1995. Ghost crab preys on piping plover eggs. Wilson Bulletin 107(4):767-768.

Weston MA, Elgar MA. 2007. Responses of incubating hooded plovers (*Thinornis rubricollis*) to disturbance. Journal of Coastal Research 23(3):569-576.

With KA, King AW. 1997. Critical thresholds in species' responses to landscape pattern. Oikos 97:219-229.

Wolcott TG. 1978. Ecological role of ghost crabs, ocypode-quadrata (Fabricius) on an ocean beach- scavengers or predators. Journal of Experimental Marine Biology and Ecology 31:67

Wolcott DL, Wolcott TG. 1999. High mortality of piping plovers on beaches with abundant ghost crabs: correlation, not causation. Wilson Bulletin 111(3):321-329.

Yasue M. 2005. The effects of human presence, flock size and prey density on shorebird foraging rates. Japan Ethological Society and Springer-Verlag Tokyo 23:199-204.

Yasue M. 2006. Environmental factors and spatial scale influence shorebirds' response to human disturbance. Biological Conservation 128:47-54.

Yasue M, Dearden P. 2006. The potential impact of tourism development on habiat availability and productivity of Malaysian plovers *Charadrius peronii*. Journal of Applied Ecology 43:978-989.
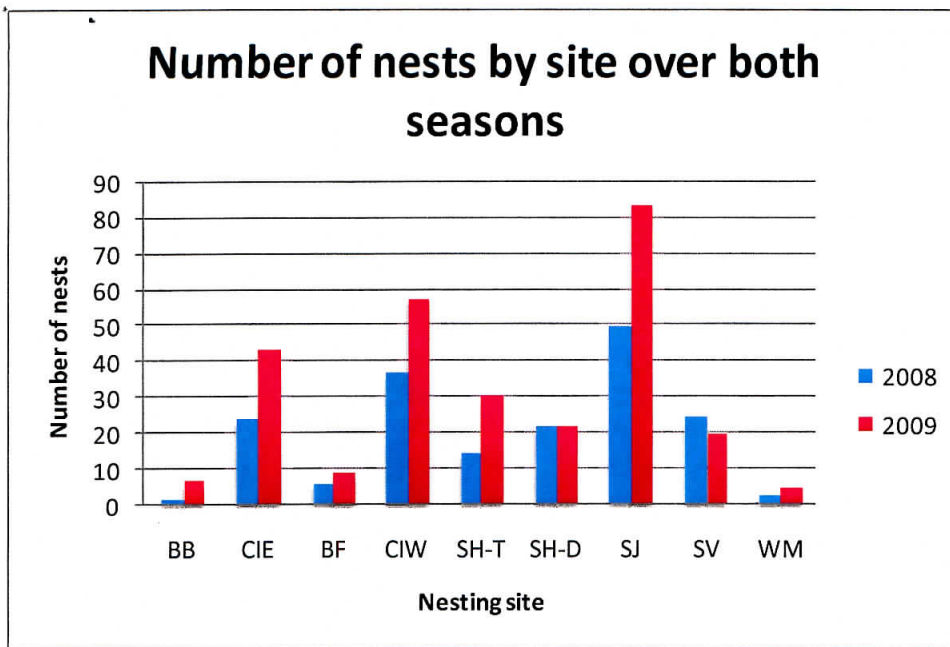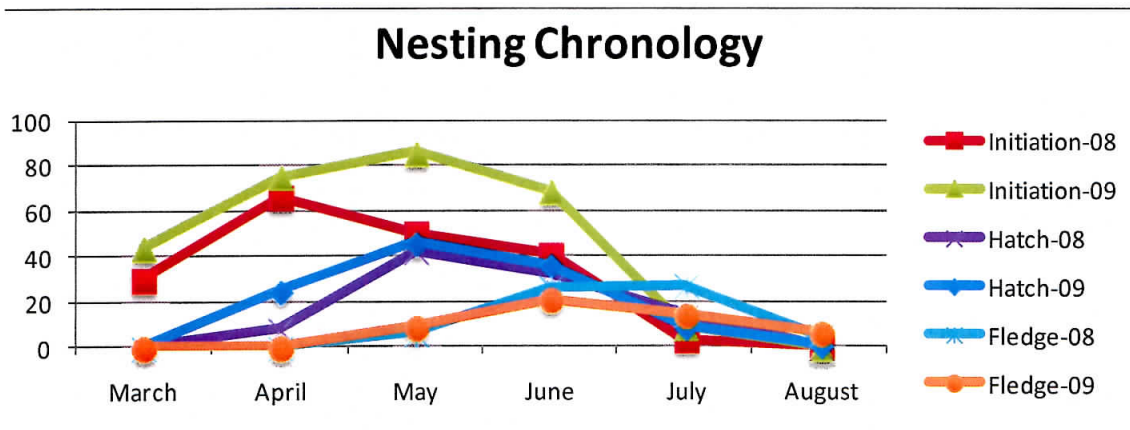
Figure 1. The number of nests by site
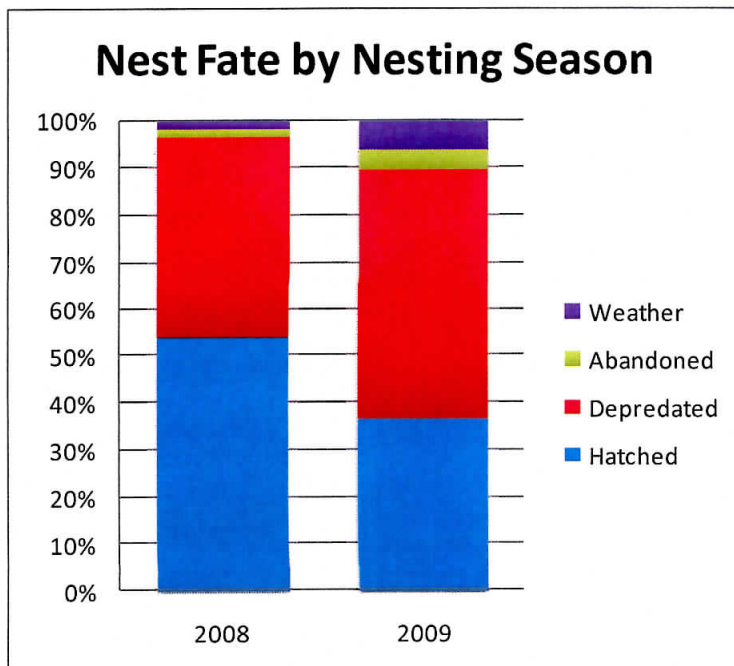

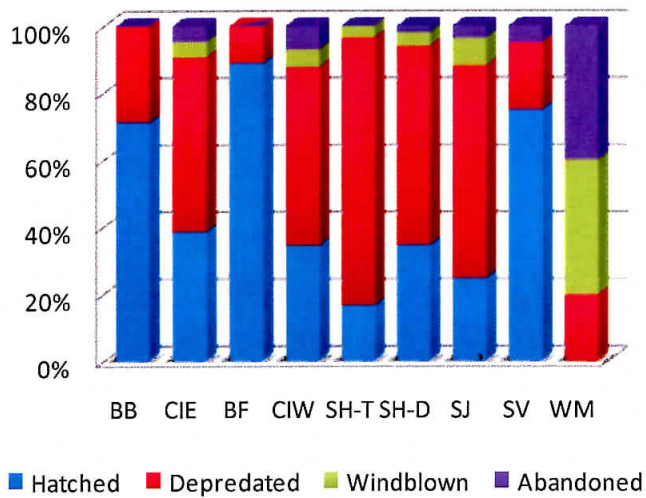Figure 2. Nesting Chronology during 2008 and 2009

Figure 3. Nest fate by season with significant difference in hatch rates.

Figure 4. Nest Fates by site separated by season.
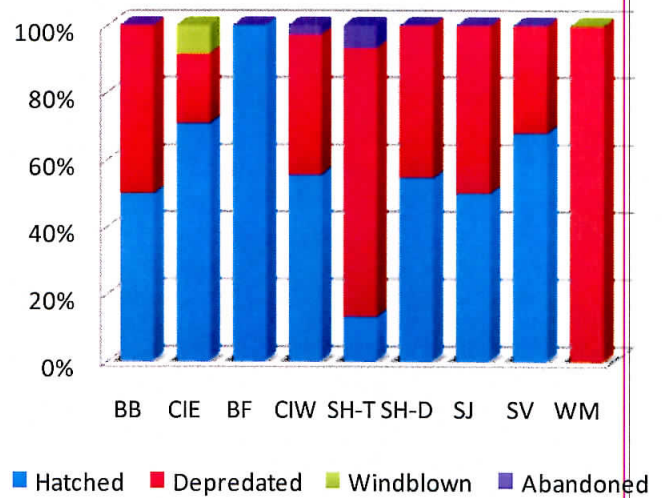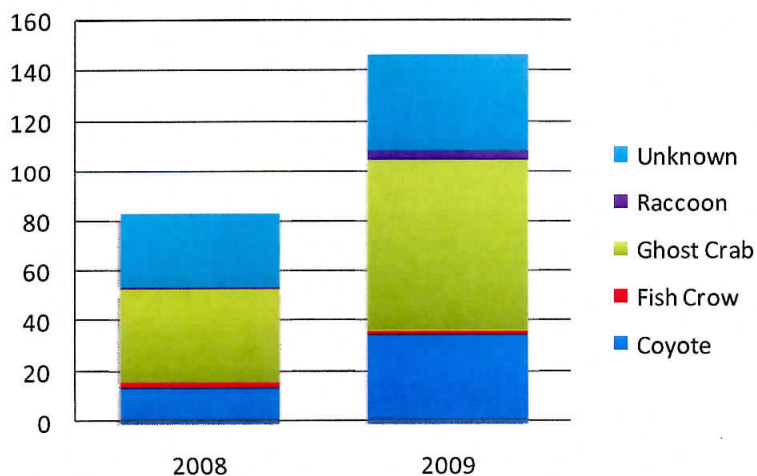

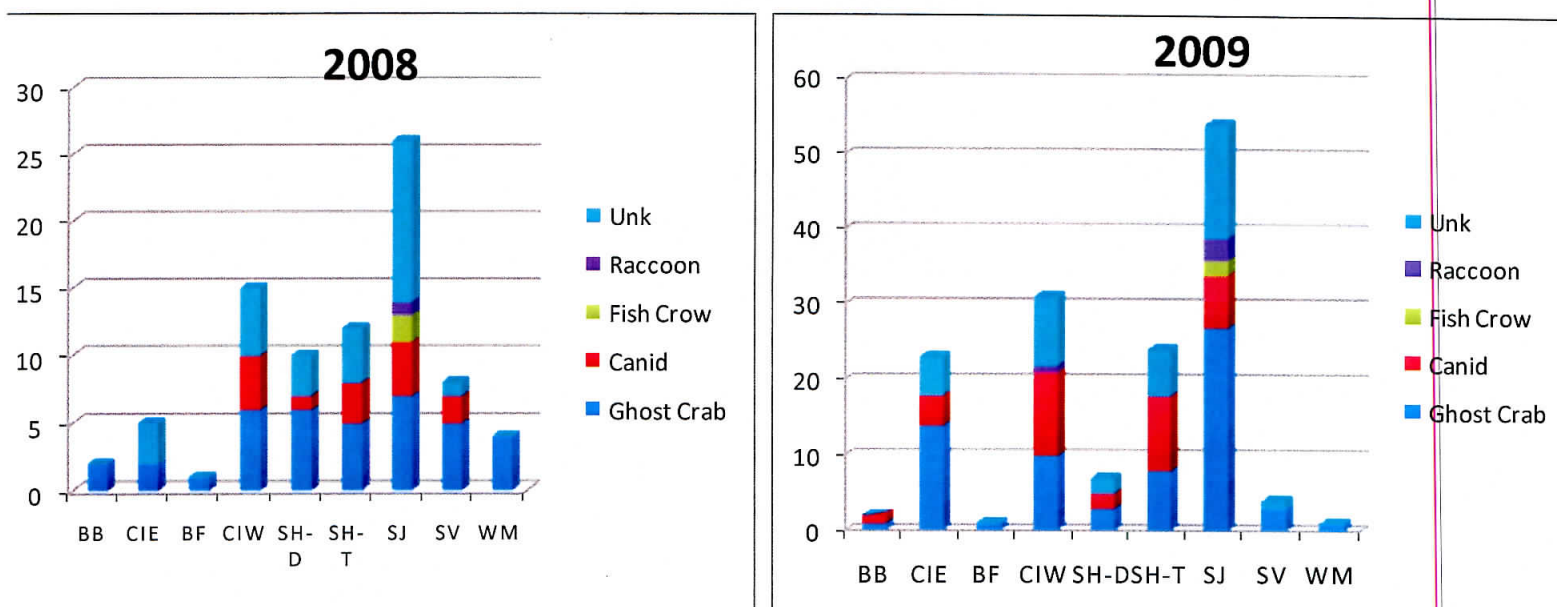Figure 5. Sources of nest depredation by season

Figure 6. Sources of depredation by site and year, greater number of predation events in 2009 at most sites.
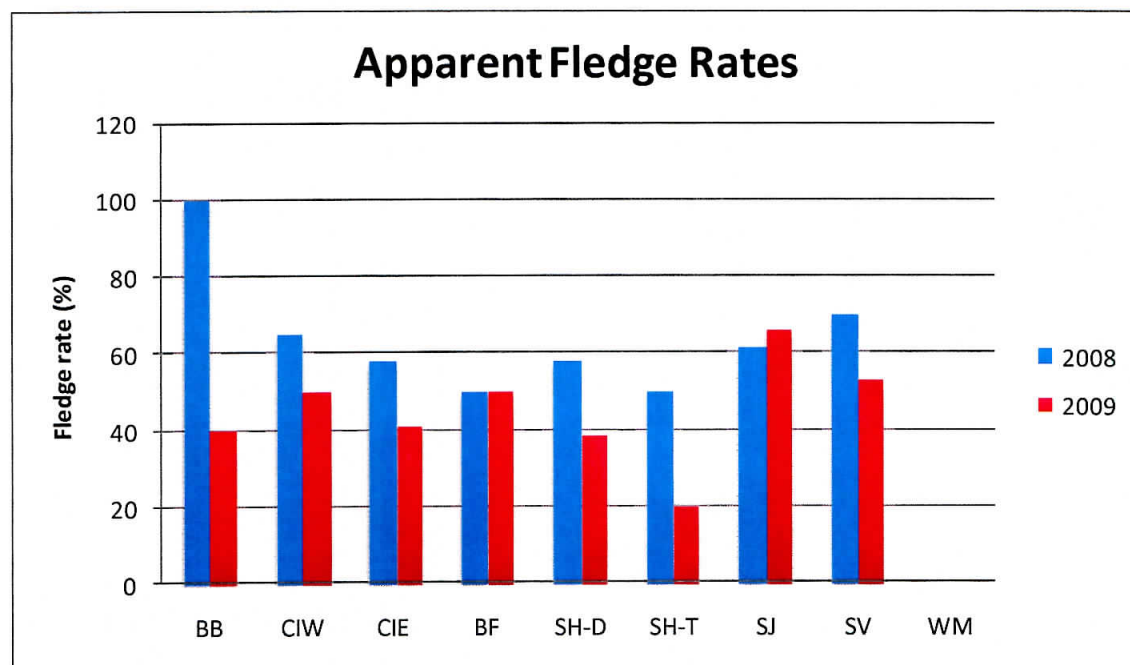

Figure 7. Apparent fledge rates by site and year. Fledge rates lower at most sites in 2009 compared to 2008.